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Leaf Traits and Resource Use Efficiencies of 19 Woody Plant Species in a Plantation in Fangshan, Beijing, China

Guowei Zhong, Yun Tian, Peng Liu, Xin Jia and Tianshan Zha *

School of Soil and Water Conservation, Beijing Forestry University, Beijing 100083, China
* Correspondence: tianshanzha@bjfu.edu.cn

Abstract: Plantations are typically monocultures, which limits their sustainability. Therefore, understanding acclimatization strategies and resource use efficiencies in plant species and life forms aids the improvement of vegetation diversity and ecological functions. Here, 19 species from forest plantations in Fangshan, Beijing, China were studied. We determined their net photosynthetic (P_n), and transpiration rates (E), light response curve, stomatal conductance (g_s), and leaf nitrogen (N) content. We analyzed the leaf N content (N_{mass}), specific leaf area (SLA), maximum net photosynthetic rate (P_{nmax}), water use (WUE), nitrogen use (NUE), and carbon use (CUE) efficiencies and connected them with both species and life forms. P_{nmax}, SLA, N_{mass}, WUE, NUE, and CUE significantly differed among species. Evergreen conifers had the lowest SLA and N_{mass} but the highest WUE and CUE. Evergreen coniferous trees had lower SLA, N_{mass}, P_{nmax}, and NUE but higher WUE than deciduous trees and shrubs. The SLA, N_{mass}, and P_{nmax} of nitrogen-fixing plants were the highest. A correlation analysis revealed that WUE was positively correlated with CUE and negatively correlated with NUE. Moreover, WUE was negatively correlated with N_{mass} and SLA. These insights into the adaptability differences of woody plant species and life forms provide a scientific basis for the selection of appropriate species for sustainable forest plantations.

Keywords: plantation; interspecific difference; leaf trait; resource use efficiency; tree; shrub

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1. Introduction

Plant functional traits are a bridge that connects plants to the environment. These traits respond to changes in the living environment and impact ecosystem functions [1,2]. Plant functional traits reflect the adaptive strategies of plants. Concurrently, differences in functional traits between either individuals or species reflect the characteristics of their habitats, i.e., species traits differ with growth environments [3,4]. Ecological filtering and competitive exclusion result from plant traits [5–7], i.e., different species within the same environment have different growth strategies [6,8].

Leaf functional traits are both an important organizational structure for energy and material exchange between plants and the environment and a major organ for photosynthesis [9]. Thus, they are a focus of plant ecology research [10–13]. Leaf functional traits are closely related to plant resource acquisition and utilization [14] and clarify plant environmental adaptability [15]. For example, leaf nitrogen content (N_{mass}) and maximum net photosynthetic rate (P_{nmax}) directly determine the photosynthetic capacity of plants. Specific leaf area (SLA) better reflects the survival strategies adapted by plants to cope with environmental changes and maximize carbon harvest [16]. At the same time, SLA affects the transpiration water losses of the plants. Leaf functional traits differ with species, functional groups, and life patterns [17,18]. For example, evergreen plants have low SLA and N_{mass}, whereas annual plants have higher P_{nmax} than perennials. Therefore, it is important to understand and predict the growth strategies and resource utilization of an entire community. These aid the determination of differences and causes thereof in leaf traits between species and life forms in the same environment.

Plants must obtain carbon, nutrients, and water from the environment for photosynthetic growth. These resource constraints influence the evolution of plant functional strategies [19]. The concept of resource use efficiency originates from the analogies between microeconomics and plant functions. The cost of carbon capture is expressed in terms of the water, nutrients, and carbon used for such functions, i.e., water use efficiency (WUE) [20], nitrogen use efficiency (NUE), and carbon use efficiency (CUE). WUE is a physiological and ecological parameter that reflects the relationship between plant material accumulation and water consumption. It is also an index for photosynthesis and transpiration in plant leaves. WUE at the leaf level is defined as the ratio of net photosynthetic to transpiration rate. NUE is a measure of leaf photosynthetic capacity under a given leaf nitrogen content and is defined as the ratio of net photosynthetic rate to leaf nitrogen content. CUE is defined as the ratio of net primary productivity (NPP) to total primary productivity (GPP) [21], which represents the potential carbon sequestration capacity of plants. This is a key factor affecting carbon storage in ecosystems. WUE, NUE, and CUE not only represent the competitive strategies of different species, but they are also important parameters for understanding the relationship between carbon, nitrogen, and water [22,23]. Due to the different plant characteristics (e.g., morphology, life history, life form), the resource utilization strategies of plants differ. WUE, NUE, and CUE in plants have clear restriction relationships [24–26]. To achieve high utilization efficiencies of restricted resources, plants adjust their functional traits [27]. Only the diversification of functional traits leads to the complementarity between species [28,29], which maximizes the efficiency of resource utilization. To understand plant resource utilization strategies in extremely harsh environments, previous studies have mainly focused on trade-offs in plant resource utilization efficiency between arid and semi-arid regions [30–32]. Conversely, there exists a paucity of studies on the adaptation differences of plants in subhumid areas, which have better water conditions, and those examining how plants utilize these resources.

Artificial forests are an important forest resource component [33] that reduces atmospheric CO_2 levels. However, the improper allocation of either single or community tree species during afforestation may decrease vegetation coverage and ecosystem function [34]. Therefore, interspecific comparative analyses of leaf functional traits and resource utilization are key to maintaining both species diversity and the sustainable development of plantation communities. The main aim of this study was to explore the resource utilization strategies among different species in the subhumid area and the relationships among carbon, nitrogen, and water in the plantation ecosystem. We hypothesized that (1) leaf functional traits and resource use efficiencies significantly differ among species and life forms in the plantation, and (2) significant correlations exist between leaf functional traits and resource use efficiencies in the plantation. Our findings provide insights into both the adaptive differences of different species in subhumid plantations and the rational allocation of plantation species.

2. Materials and Methods

2.1. Study Site

The study area was in Beijing Fangshan Qinglong Lake Artificial Forest Ecological Monitoring Station. The experimental station was in Fangshan Qinglong Lake Artificial Forest Park Wan Mu (39.78° N, 116.04° E), at an altitude of 93 m. The area had a typical semi-humid monsoon climate in the warm temperate zone. The average annual precipitation was about 595 mm, which was unevenly distributed between June and August. The annual average temperature was about 10 °C with highs and lows of 42 °C and −27.4 °C, respectively. The frost-free period was 190–210 days. The annual average wind speed was 2.3 m/s, and the wind direction changed considerably. The study area was dominated by plantation forests. The predominant tree species were *Populus tomentosa*, *Rhus typhina*, *Malus spectabilis*, *Prunus davidiana* and *Ulmus pumila* 'Jinye', *Styphnolobium japonicum*, *Fraxinus chinensis*, *Crataegus pinnatifida*, *Prunus cerasifera* 'Atropurpurea', *Robinia pseudoacacia*, *Prunus armeniaca*, *Yulania denudata*, *Amorpha fruticosa*, *Cotinus Coggygria*, *Forsythia suspensa*, *Euonymus japonicus* 'Aureo-marginatus', *Pinus bungeana*, *Pinus tabuliformis*, and *Platycladus orientalis* (Table 1).

Table 1. List of the 19 species in the plantation in Qinglonghu, Beijing.

Life Form		**Species**	**Family**	**Height H/m**	**Breast Diameter B/cm**	**Stand Age S/years**	**Central Latitude and Longitude**	**Elevation/m**
Tree	Deciduous trees	*Rhus typhina*	Anacardiaceae	5.16	12.01	8	116°2′5″ E, 39°46′29″ N	95
	Deciduous trees	*Malus spectabilis*	Rosaceae	3.54	10.54	8	116°2′10″ E, 39°46′19″ N	100
	Deciduous trees	*Prunus davidiana*	Rosaceae	5.94	8.76	8	116°2′25″ E, 39°46′8″ N	110
	Deciduous trees	*Ulmus pumila* 'Jinye'	Ulmaceae	4.63	11.81	8	116°2′27″ E, 39°46′46″ N	100
	Deciduous trees	*Fraxinus chinensis*	Oleaceae	5.37	9.16	8	116°2′1″ E, 39°46′26″ N	100
	Nitrogen fixing plant	*Styphnolobium japonicum*	Leguminosae	6.08	7.52	8	116°2′1″ E, 39°46′31″ N	100
	Deciduous trees	*Crataegus pinnatifida*	Rosaceae	2.5	7.86	8	116°1′41″ E, 39°46′35″ N	100
	Deciduous trees	*Prunus cerasifera* 'Atropurpurea'	Rosaceae	4.68	11.28	8	116°2′2″ E, 39°46′41″ N	90
	Nitrogen fixing plant	*Robinia pseudoacacia*	Leguminosae	6.24	9.69	8	116°1′46″ E, 39°46′26″ N	110
	Deciduous trees	*Populus tomentosa.*	Salicaceae	6.93	12.3	8	116°2′16″ E, 39°46′44″ N	100
	Deciduous trees	*Prunus armeniaca*	Rosaceae	5.52	18.25	8	116°2′10″ E, 39°46′19″ N	80
	Deciduous trees	*Yulania denudata*	Magnoliaceae	3.24	25.7	8	116°2′10″ E, 39°46′19″ N	95
	Evergreen conifer	*Pinus bungeana*	Pinaceae	3.65	16.56	8	116°2′13″ E, 39°46′18″ N	110
	Evergreen conifer	*Pinus tabuliformis*	Pinaceae	3.07	8.07	8	116°2′13″ E, 39°46′18″ N	110
	Evergreen conifer	*Platycladus orientalis*	Cupressaceae	4.62	9.55	8	116°2′26″ E, 39°46′40″ N	95
Shrub	Nitrogen fixing plant	*Amorpha fruticosa*	Leguminosae	2.04	4.25	8	116°2′26″ E, 39°46′44″ N	95
	Deciduous shrub	*Cotinus coggygria*	Anacardiaceae	3.25	7.26	8	116°2′27″ E, 39°46′44″ N	95
	Deciduous shrub	*Forsythia suspensa*	Oleaceae	0.74	2.55	8	116°2′13″ E, 39°46′18″ N	110
	Deciduous shrub	*Euonymus japonicus* 'Aureo-marginatus'	Celastraceae	0.65	2.12	8	116°2′10″ E, 39°46′19″ N	100

2.2. Methods

2.2.1. Measurement of the Light Response Curves

Nineteen afforestation species were studied in the 10,000 mu plantation park of Qinglong Lake in Fangshan (Table 1). During the selection of sample plots, since the local species were all artificially cultivated, the distance between trees was the same, and the plot was regular. Therefore, we selected 19 flat plots near the flux tower as the study area. In nineteen 20 m × 20 m pure forest plots, three healthy trees of uniform growth and devoid of pests and diseases were sampled for each species. From each sample plant, three leaves with good light exposure, healthy growth, and no pests and diseases were selected. The fluorescence leaf chamber of a portable photosynthesizing apparatus (LI-6800, Li-Cor Inc., Lincoln, NE, USA) was used to measure the light response curve on a typical sunny day of the 2021 growing season. The measuring time was from 8:30 a.m. to 11:30 a.m. An open gas path was used, the relative humidity was set to 50%, the CO$_2$ concentration was set to 400 µmol·mol^{-1}, the leaf chamber temperature was set to 25 °C, and the light intensity gradient consisted of 12 points. They were 1800, 1500, 1200, 900, 600, 300, 200, 150, 100, 70, 30, and 0 µmol·m^2·s^{-1}. The leaves were spread out and then stacked to fill the whole leaf chamber. After 2–3 min of adaptation under each photosynthetically active radiation level, the net photosynthetic rate (P_n) was measured to one decimal place. The transpiration rate (E), stomatal conductance (g_s), photosynthetically active radiation (I), and intercellular CO_2 concentration (C_i) were also measured. After measuring the gas exchange parameters, if the measured plant leaf area was less than the leaf chamber area (6 cm^2), leaves were taken to the laboratory for photography to calculate leaf areas and the gas exchange values by MATLAB (R2020b, MathWorks, USA). The photosynthetic parameters (maximum net photosynthetic rate, dark respiration rate, and apparent quantum efficiency) were obtained by model fitting.

2.2.2. Determination of Leaf Traits

The sampled plants were assessed for light response measurements. For each plant, 10–20 fully extended leaves of similar size, under good light exposure and with typical healthy growth, were selected. In the laboratory, the leaf area was measured with a portable leaf area instrument (LI-3000C, Li-Cor Inc., Lincoln, NE, USA). For each leaf, three values were calculated, which were then averaged. Concurrently, the fresh weight of the plant leaves was determined, and the leaves were dried at 108 °C for 15 min, and then dried at 75 °C for 48 h to a constant mass. The dry weight was determined. The specific leaf area (SLA) was the ratio of leaf area to dry weight. The dried leaves were ground and stored in zip-lock bags. The species information and sampling date were marked on the sample bags. The samples were assessed by the Beijing Academy of Agriculture and Forestry Sciences for the nitrogen content (N_{mass}) of leaves by the Kjeldahl nitrogen determination method. Subsequently, the nitrogen content per unit area (N_{area}) was calculated.

2.3. Data Processing

2.3.1. Calculation of Leaf Functional Traits and Resource Utilization Efficiency

A mechanistic model was used, which was based on the maximum net photosynthetic rate of plant leaves based on the response of plant photosynthesis to light (modified rectangular hyperbola model) [35,36]. Use the following formula to calculate the result (Table 2). The model equation was:

$$P_n = \alpha \frac{1-\beta I}{1+\gamma I} I - R_d \tag{1}$$

where α is the initial slope of the light response curve and represents apparent quantum efficiency, β and γ are correction coefficients (unit: $m^2 \cdot s \cdot \mu mol^{-1}$), I is photosynthetically active radiation, and R_d is dark respiration rate. The saturated light intensity (I_{sat}) and maximum net photosynthetic rate (P_{nmax}) of the plants were calculated according to the following formula:

$$I_{sat} = \frac{\sqrt{(\beta+\gamma)/\beta} - 1}{\gamma} \tag{2}$$

$$p_{nmax} = \alpha \left(\frac{\sqrt{\beta+\gamma} - \sqrt{\beta}}{\gamma} \right)^2 - R_d \tag{3}$$

According to the definition of WUE, Formula (3) can be used to obtain the WUE of plant leaves:

$$\mathrm{WUE} = P_{nmax}/E \tag{4}$$

where E is the transpiration rate corresponding to the maximum net photosynthetic rate of plants.

Nitrogen content per unit leaf area:

$$N_{area} = N_{mass}/SLA \tag{5}$$

The calculation formula for nitrogen utilization efficiency is:

$$\text{NUE} = P_{nmax} / N_{area} \tag{6}$$

The calculation formula for carbon utilization efficiency is:

$$\text{CUE} = \frac{P_{nmax}}{P_{nmax} + R_d} \tag{7}$$

Table 2. The maximum net photosynthetic rate (P_{nmax}), specific leaf area (SLA), leaf nitrogen content (N_{mass}), water use efficiency (WUE), nitrogen use efficiency (NUE), and carbon use efficiency (CUE) of 19 species from the mixed plantation in Qinglonghu, Beijing (mean ± SE).

Species	**P_{nmax} (μmol·m^2·s^{-1})**	**SLA (cm^2·g^{-1})**	**N_{mass} (g/kg)**	**WUE (mmol·mol^{-1})**	**NUE (μmol·g^{-1}·s^{-1})**	**CUE (%)**
Rhus typhina	26.09 ± 0.41	146.6 ± 29.58	35.88 ± 0.23	4.64 ± 0.36	10.66 ± 0.17	88.6 ± 0.35
Malus spectabilis	22.6 ± 3.07	129.5 ± 25.98	21.06 ± 0.46	3.58 ± 0.07	13.9 ± 1.13	84.2 ± 0.67
Prunus davidiana	20.64 ± 0.62	135.3 ± 32.63	24.12 ± 0.25	3.63 ± 0.2	11.58 ± 1.12	86.8 ± 1.96
Ulmus pumila 'Jinye'	21.95 ± 2.01	202.2 ± 64.29	32.64 ± 0.35	4.01 ± 0.34	13.6 ± 1.25	85.2 ± 0.45
Fraxinus chinensis	18.31 ± 0.59	143.4 ± 33.06	21.16 ± 0.27	2.78 ± 0.29	9.66 ± 0.31	81.1 ± 2.61
Styphnolobium japonicum	15.81 ± 0.3	149.5 ± 48.43	22.9 ± 0.25	5.14 ± 0.64	9.9 ± 0.16	86.2 ± 3.99
Crataegus pinnatifida	17.34 ± 1.14	94.2 ± 11.15	18.33 ± 0.16	3.52 ± 0.38	8.91 ± 1.17	87.6 ± 1.08
Prunus cerasifera 'Atropurpurea'	15.4 ± 0.81	237.6 ± 125.38	21.56 ± 0.14	2.91 ± 0.36	16.97 ± 3.82	85.5 ± 1.38
Robinia pseudoacacia	16.02 ± 2.09	149.5 ± 31.28	20.34 ± 0.22	3.4 ± 0.68	11.77 ± 2.27	84.9 ± 1.94
Populus tomentosa	12.98 ± 0.62	123.3 ± 26.24	22.13 ± 0.07	3.8 ± 0.71	7.23 ± 1.32	80.7 ± 1.05
Prunus armeniaca	11.32 ± 1.21	162.3 ± 15.72	22.17 ± 0.23	4.89 ± 1.07	8.29 ± 0.88	85.4 ± 1.27
Yulania denudata	6.72 ± 0.14	150 ± 22.58	19.02 ± 0.2	4.95 ± 1.46	5.3 ± 2.08	84.4 ± 0.36
Pinus bungeana	20.87 ± 2.3	39 ± 4.04	12.58 ± 0.35	7.84 ± 2.4	6.2 ± 0.69	85.8 ± 2.09
Pinus tabuliformis	19.26 ± 0.46	41 ± 8.05	14.29 ± 2.95	9.11 ± 1.35	5.89 ± 0.14	94.8 ± 1.67
Platycladus orientalis	10.6 ± 0.76	79 ± 9.61	11.11 ± 1.38	5.38 ± 0.94	7.14 ± 0.51	71.9 ± 2.45
Amorpha fruticosa	28.92 ± 1.6	217.4 ± 22.46	38.8 ± 1.32	3.21 ± 0.62	12.9 ± 0.72	83.6 ± 2.11
Cotinus coggygria	15.84 ± 2.79	125.4 ± 15.28	21.8 ± 1.0	6 ± 1.1	9.34 ± 1.65	87.2 ± 1.54
Forsythia suspensa	23.67 ± 0.06	135.9 ± 21.06	15.8 ± 2.5	3.2 ± 0.22	15.58 ± 0.04	82.4 ± 1.87
Euonymus japonicus 'Aureo-marginatus'	10.6 ± 3.79	122 ± 15.28	25.8 ± 3.25	2.54 ± 1.64	6.86 ± 1.79	76.5 ± 4.56

2.3.2. Data Analysis

The experimental data for the measured light response curves were analyzed in Microsoft Excel (2021, Microsoft, Redmond, WA, USA), whereas the correction model of the rectangular hyperbola was created in MATLAB 2021. The statistical significance of differences in P_{nmax}, SLA, N_{mass}, WUE, NUE, and CUE among species was analyzed by a one-way ANOVA (one-way ANOVA, $p = 0.05$). Least squares difference (LSD) post hoc tests were conducted to identify significant differences between means. Correlations between leaf functional traits and resource utilization efficiency were determined by a simple linear model. All the drawings were made in Origin 2021 software.

3. Results

3.1. Interspecific Differences in Leaf Functional Traits and Resource Use Efficiency

3.1.1. Interspecific Differences of Leaf Functional Traits

The P_{nmax} of 19 species was between 6 and 29 μmol·m^2·s^{-1}, and significantly differed with species ($p < 0.05$, Table 3). The highest P_{nmax} (28.92 ± 1.6 μmol·m^2·s^{-1}) was of a nitrogen-fixing legume, whereas the lowest was of a southern species, *Yulania denudate* (6.72 ± 0.14 μmol·m^2·s^{-1}). Fourteen out of nineteen (73.7%) species had P_{nmax} values above 15 μmol·m^2·s^{-1} (Figure 1A).

The SLA for the 19 species was between 39 and 238 cm^2·g^{-1} and significantly differed with species ($p < 0.05$, Table 3). The SLA for four species was less than 100 cm^2·g^{-1}: *Pinus bungeana* (39 cm^2·g^{-1}), *Pinus tabuliformis* (41 cm^2·g^{-1}), *Platycladus orientalis* (79 cm^2·g^{-1}), and *Crataegus pinnatifida* (94.2 cm^2·g^{-1}). Thirteen species had an SLA between 100 and 200 cm^2·g^{-1}, while two species had an SLA greater than 200 cm^2·g^{-1}: *Ulmus pumila* 'Jinye' (202.2 cm^2·g^{-1}) and *Prunus cerasifera* 'Atropurpurea' (237.6 cm^2·g^{-1}) (Figure 1B).

Table 3. Analysis of variance of leaf functional traits and resource utilization efficiencies of different species.

Variable	ANOVA Sum of Squares	df	Mean Square	F
WUE	136.83	18	7.6	8.7 ***
CUE	1125	18	62.5	14.6 ***
NUE	530.13	18	29.45	15.26 ***
P_{nmax}	1657.38	18	92.08	20.79 ***
SLA	288,360.43	18	16,020.02	5.92 ***
N_{mass}	5637.81	18	313.21	55.32 ***

Note: *** indicate $p < 0.001$.

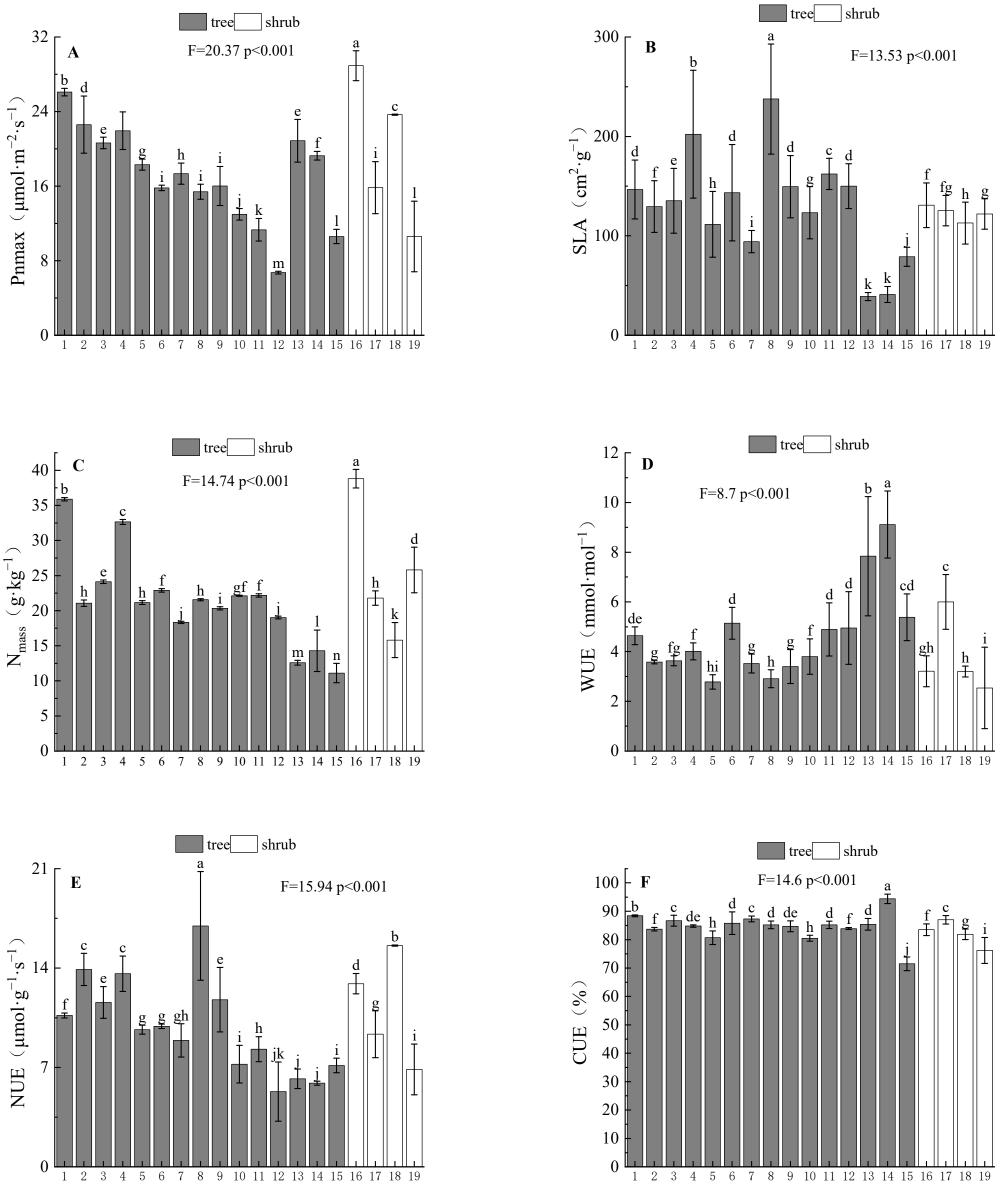

Figure 1. Comparison of mean value of maximum net photosynthetic rate (P_{nmax}, (**A**)), specific leaf area (SLA, (**B**)), leaf nitrogen content (N_{mass}, (**C**)), water use efficiency (WUE, (**D**)), nitrogen use efficiency (NUE, (**E**)), and carbon use efficiency (CUE, (**F**)) among different species (mean ± SE). Different small letters indicate significant difference between life forms for the same resource utilization efficiency ($p < 0.05$).

The distribution of N_{mass} in the leaves of the 19 species ranged from 11 to 40 g/kg. The N_{mass} of *Rhus typhina*, *Ulmus pumila* 'Jinye', and *Amorpha denudated* was higher (>30 g/kg). The N_{mass} of *Pinus bungeana*, *Platycladus orientalis*, and *Pinus tabuliformis* was low (<15 g/kg) (Figure 1C).

3.1.2. Interspecific Differences in Leaf Resource Utilization Efficiency

The WUE of the leaves of the 19 species ranged from 2.54 to 9.11 mmol·mol^{-1} and significantly differed with species ($p < 0.05$, Table 3). Three species had a WUE below 2 mmol·mol^{-1}, and 14/19 species (73.7%) had a WUE between 3 and 6 mmol·mol^{-1}. Only two species had a WUE above 7 mmol·mol^{-1}. The WUE of *Euonymus japonicus* 'Aureo-marginatus' was the lowest at 2.54 mmol·mol^{-1}, whereas that of a member of the WUE of *Pinaceae* was 7.84 and 9.11 mmol·mol^{-1}, and *Pinus tabulaeformis* had the highest values (Figure 1D).

The NUE ranged from 5.3 to 16.97 µmol·g^{-1}·s^{-1} and significantly differed with species ($p < 0.05$, Table 3). The NUE of *Yulania denudate*, *Pinus bungeana*, *Pinus tabuliformis*, and *Euonymus japonicus* 'Aureo-marginatus' was lower than 7 µmol·g^{-1}·s^{-1}. The NUEs of *Rhus typhina*, *Malus spectabilis*, *Prunus davidiana*, *Ulmus pumila* 'Jinye', *Prunus cerasifera* 'Atropurpurea', *Robinia pseudoacacia*, *Amorpha fruticose*, and *Forsythia suspensa* were above 10 µmol·g^{-1}·s^{-1}, accounting for 42% of the total number of species (Figure 1E). The NUE of *Yulania denudate* was the lowest (5.3 µmol·g^{-1}·s^{-1}), and that of *Prunus cerasifera* 'Atropurpurea' was the highest (16.97 µmol·g^{-1}·s^{-1}), which was nearly three times that of *Yulania denudate*.

The CUE of different species ranged from 71.9% to 94.8%. The highest CUE was *Pinus tabulaeformis* (94.8%), and the lowest was *Platyclus orientalis* (71.9%). The CUE of other plants was between 80% and 89%, accounting for 89.5% of the total number of species (Figure 1F).

Abscissa species: 1, *Rhus typhina*; 2, *Malus spectabilis*; 3, *Prunus davidiana*; 4, *Ulmus pumila* 'Jinye'; 5, *Styphnolobium japonicum*; 6, *Fraxinus chinensis*; 7, *Crataegus pinnatifida*; 8, *Prunus cerasifera* 'Atropurpurea'; 9, *Robinia pseudoacacia*; 10, *Populus tomentosa*; 11, *Prunus armeniaca*; 12, *Yulania denudata*; 13, *Pinus bungeana*; 14, *Pinus tabuliformis*; 15, *Platycladus orientalis*; 16, *Amorpha fruticosa*; 17, *Cotinus coggygria*; 18, *Forsythia suspensa*; 19, *Euonymus japonicus* 'Aureo-marginatus'. Species 1–15 are trees and 16–19 are shrubs.

3.2. Differences in Life Forms

Leaf functional traits and resource use efficiency at the life form level significantly differed. Among the four life forms, the functional traits (SLA, P_{nmax}, N_{mass}) of evergreen conifers were significantly lower than those of deciduous trees and shrubs, and nitrogen fixing plants ($p < 0.05$, Figure 2). The WUE of evergreen conifers was significantly higher than that of other life forms ($p < 0.05$, Figure 3). The SLA, P_{nmax}, and N_{mass} of nitrogen-fixing plants were significantly higher than those of other life forms ($p < 0.05$, Figure 2). There was no significant difference in functional traits between deciduous trees and deciduous shrubs. Moreover, their values were both between those of evergreen conifers and nitrogen-fixing plants.

The WUE of evergreen conifers (7.24 mmol·mol^{-1}) was significantly higher than that of deciduous shrubs ($p < 0.01$, Figure 3). The WUE of deciduous trees was 3.87 mmol·mol^{-1} and that of deciduous shrubs was 3.74 mmol·mol^{-1}. The CUE of evergreen conifers and deciduous shrubs did not significantly differ ($p > 0.05$; Figure 3). The NUE of deciduous trees and deciduous shrubs were significantly higher than that of evergreen conifers ($p < 0.01$, Figure 3). The NUE of both species of deciduous trees was above 10 µmol·g^{-1}·s^{-1}, whereas that of the latter was below 7 µmol·g^{-1}·s^{-1}.

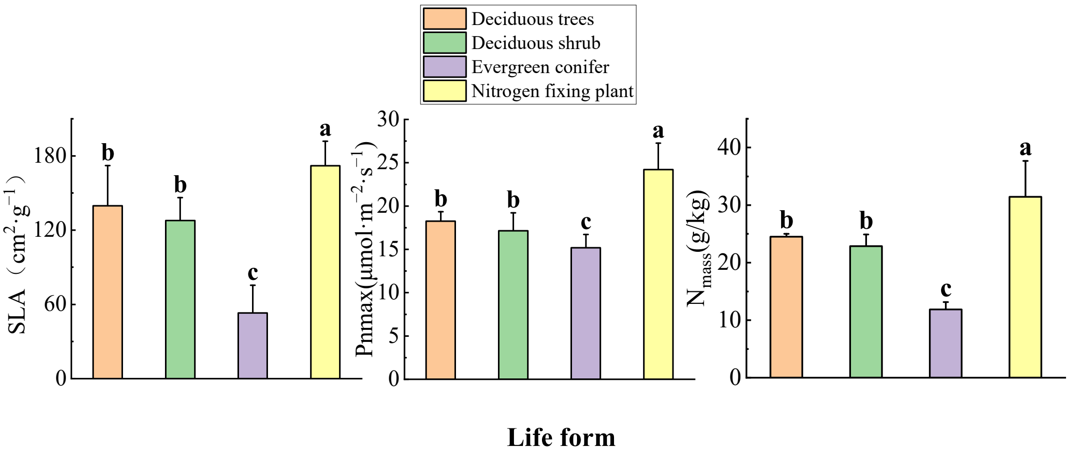

Figure 2. Comparison of mean value of maximum net photosynthetic rate (P_{nmax}), specific leaf area (SLA), and leaf nitrogen content (N_{mass}) between life forms (mean ± SE). Different small letters indicate significant difference between life forms for a given trait ($p < 0.05$).

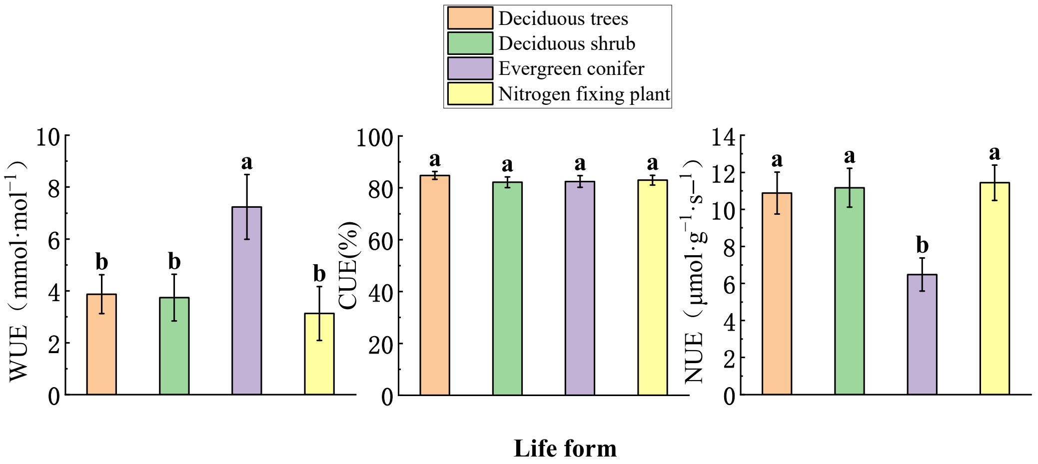

Figure 3. Comparison of mean value of water use efficiency (WUE), nitrogen use efficiency (NUE), and carbon use efficiency (CUE) between life forms (mean ± SE). Different small letters indicate significant difference between life forms for the same resource utilization efficiency ($p < 0.05$).

3.3. Correlations between Resource Use Efficiency and Leaf Functional Traits

At the species level, WUE was significantly correlated with CUE (Figure 4, $p < 0.01$), and significantly negatively correlated with NUE (Figure 4, $p < 0.001$); CUE and NUE were not significantly correlated. For leaf functional traits, WUE was significantly correlated with SLA and N_{mass} (Figure 5, $p < 0.01$). An increase in SLA and N_{mass} resulted in a decrease in WUE. The response of WUE to P_{nmax} was not clear. CUE and NUE were positively correlated with P_{nmax} (Figure 5, $p < 0.01$). The R^2 value between NUE and P_{nmax} was larger than that between CUE and P_{nmax}, indicating a stronger correlation. In this study, P_{nmax} was significantly positively correlated with R_d in different plants (Figure 6, $p < 0.01$), and the greater the P_{nmax}, the greater the R_d. Moreover, there was a significant negative correlation between CUE and R_d (Figure 6, $p < 0.05$).

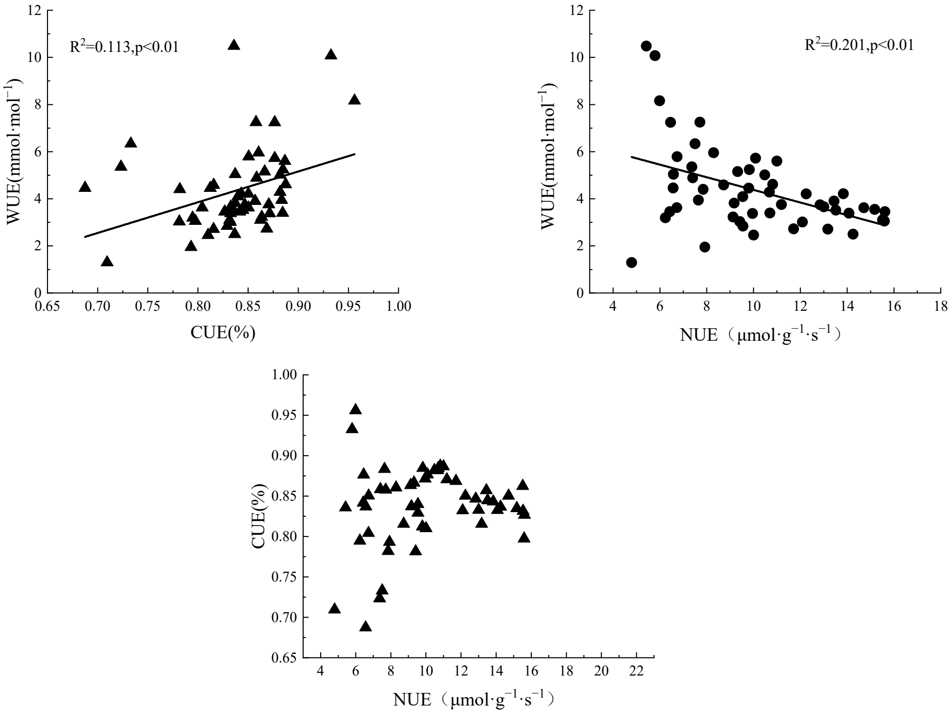

Figure 4. Relationship between resource utilization efficiencies.

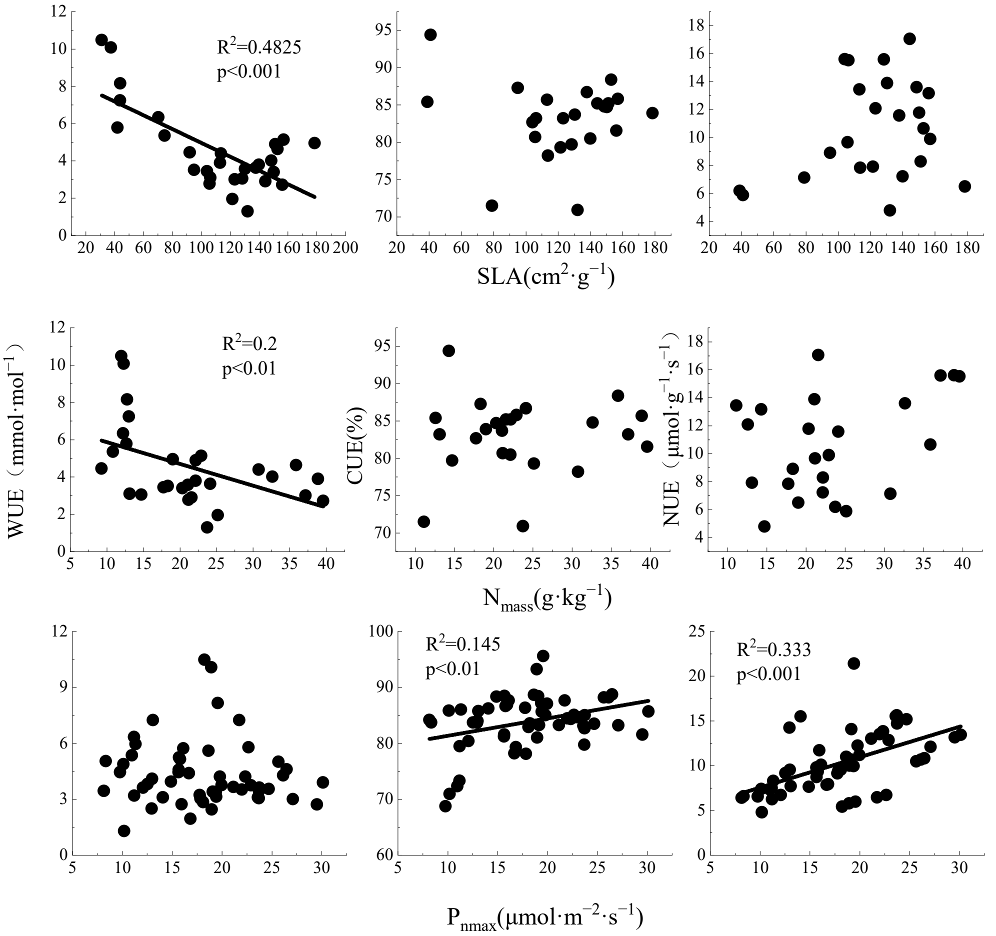

Figure 5. Relationship between specific leaf area (SLA), leaf nitrogen content (N_{mass}), maximum net photosynthetic rate (P_{nmax}), and resources utilization efficiencies.

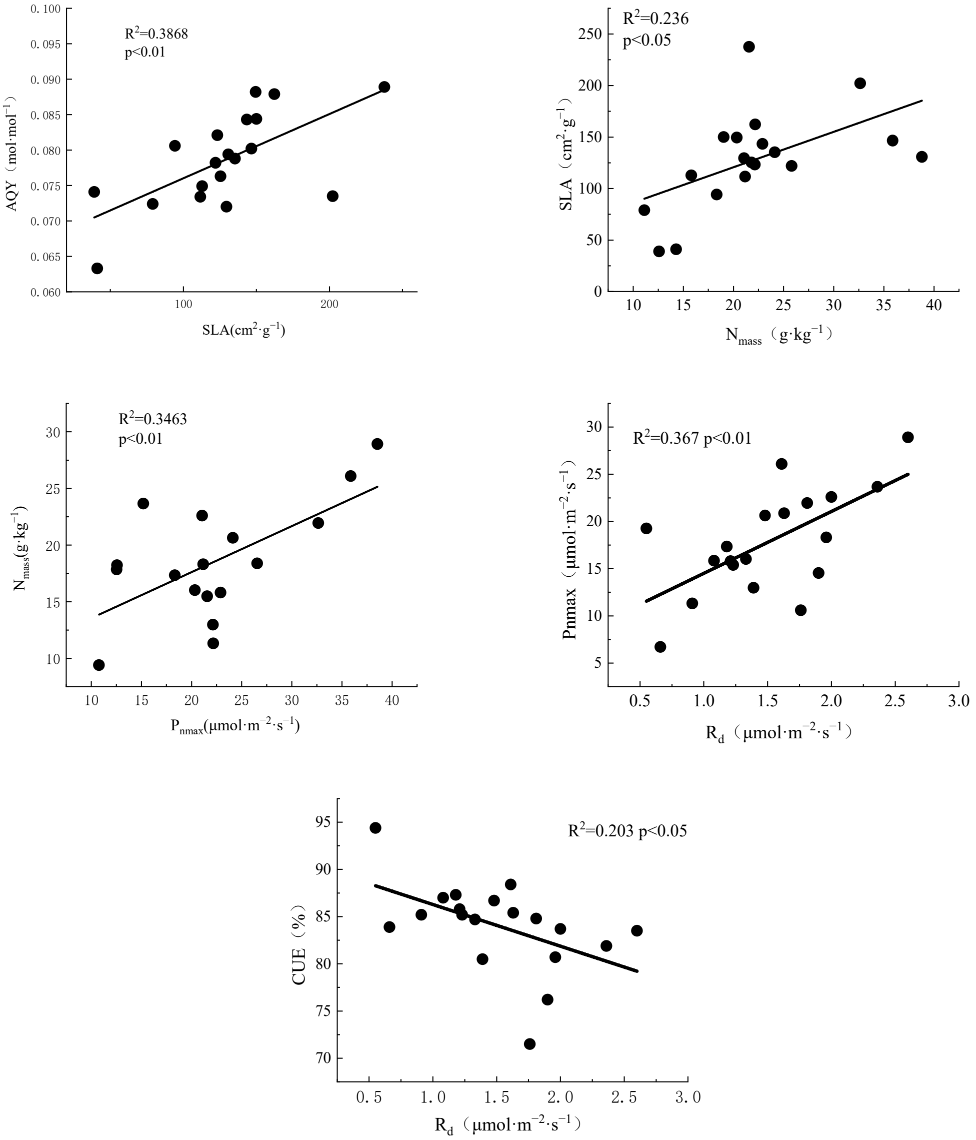

Figure 6. Relationship between specific leaf area (SLA) and apparent quantum yield (AQY), leaf nitrogen content (N_{mass}) of different species. Relationship between leaf nitrogen content (N_{mass}) and maximum net photosynthetic rate (P_{nmax}) of different species. Relationship between dark respiratory rate (R_d) and maximum net photosynthetic rate (P_{nmax}), carbon use efficiency (CUE) of different species.

3.4. Principal Component Analyses

The results of the principal component analysis showed that the interpretation rates of principal component 1 and principal component 2 were 47.16% and 25.9%, respectively, with a total of 73.06%. Principal component 1 had a high correlation with SLA, N_{mass}, and NUE, which all had a positive correlation. Principal component 2 was highly correlated with WUE, CUE, and P_{nmax}, which all had a positive correlation (Figure 7, Table 4). As shown in Figure 7, evergreen coniferous trees are located in the negative area of the first principal component axis and the second principal component axis, with higher WUE and CUE. Nitrogen fixing plants are mainly located in the positive part of the first principal component axis, with higher N_{mass}, NUE, and SLA. Deciduous trees and deciduous shrubs are partly distributed in the positive area of the main axis and partly in the negative area.

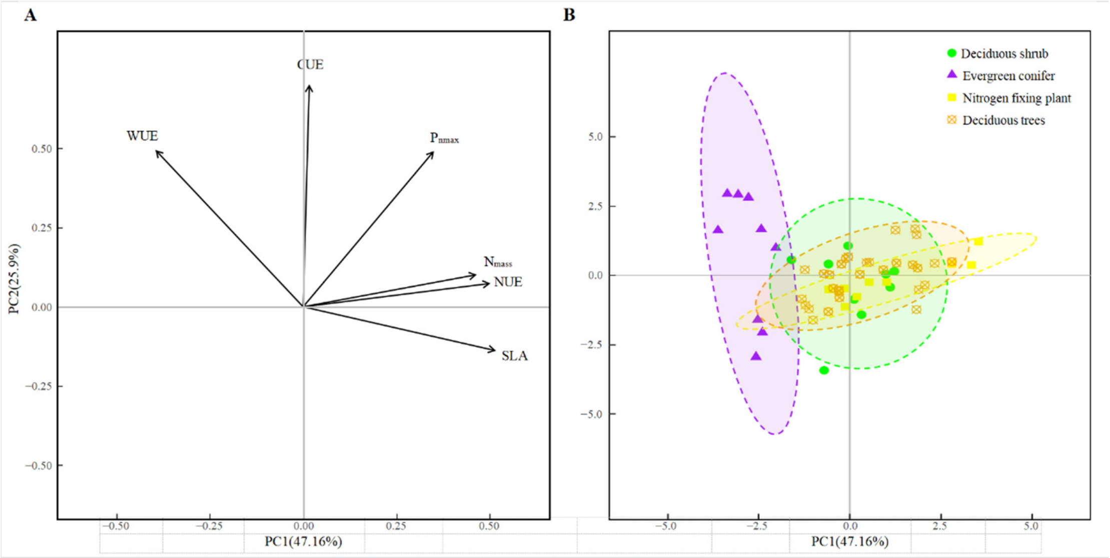

Figure 7. Results of principle component (PC) analyses of leaf traits and resource utilization efficiencies. (**A**) Main trait loads. (**B**) Response of traits to different life forms.

Table 4. Loadings and interpreted variance of leaf traits and resource utilization efficiencies in principal components analyses.

Traits	Principal Component 1	Principal Component 2
P_{nmax}	0.35	0.49
SLA	0.51	−0.14
N_{mass}	0.46	0.1
WUE	−0.39	0.49
CUE	0.02	0.69
NUE	0.49	0.07
Variance ratio	47.16%	25.9%
Cumulative variance ratio	47.16%	73.06%

4. Discussion

4.1. Differences in Leaf Functional Traits and Resource Utilization Efficiency of Different Species

There are considerable intraspecific and interspecific differences in leaf functional traits (such as SLA, P_n, and N_{mass}) even for plants in very similar environments [11,13]. This is hypothesized to result from long-term natural selection [37]. From the analysis of three leaf functional traits of 19 species in Fangshan, Beijing, P_{nmax}, SLA, and N_{mass} significantly differed among plants in the same habitat, indicating that plants adapted differently to the same environment.

Specific leaf area is a key indicator of leaf functional traits, which reflects the trade-offs of the carbon acquisition, growth, and adaptation strategies of plants under different resource environments [38]. Plants with high SLA have high productivity and adapt easily to resource-rich environments; however, plants with low SLA are well-adapted to resource-poor environments [38,39]. Among the 19 species investigated, the average SLA was 163.32 $cm^2 \cdot g^{-1}$, among which the smallest were for *Pinus bungeana* (39 $cm^2 \cdot g^{-1}$) and Pinus tabulaeformis (41 $cm^2 \cdot g^{-1}$), and the largest was for the *Prunus cerasifera* 'Atropurpurea' (237.6 $cm^2 \cdot g^{-1}$). Accordingly, plants with low SLA, such as *Pinus tabulaeformis* and *Pinus bungeana*, should dominate in relatively dry areas, whereas plants with high SLA, such as *Prunus cerasifera* 'Atropurpurea', should dominate in the relatively humid areas, which supports the restoration of the regional ecosystem and increase in ecosystem biomass. Qinglonghu Plantation Park in Beijing is in a semi-humid area at circa 100 m above sea level. It is characterized by a warm temperate semi-humid monsoon climate in summer and cold dry winters. Such climatic characteristics shaped the specificity of plant functional traits in this area. For example, in this study, SLA—the central characteristic of leaf morphology—fully reflected the climatic characteristics. The SLA (23.54 $cm^2 \cdot g^{-1}$ and 25.15 $cm^2 \cdot g^{-1}$) of *Pinus tabulaeformis* and *Platycladus orientalis* in the Huoshan area of Shanxi Province [40] was significantly lower than that of *Pinus tabulaeformis* and *Platycladus orientalis* in similar subhumid areas but at altitudes above 2000 m. Species here had high water and nutrient element contents. SLA significantly differed between the semi-arid (158.1 $cm^2 \cdot g^{-1}$) and humid areas (close to 400 $cm^2 \cdot g^{-1}$) [8,41]. The SLA of *Amorpha fruticosa* in this study area was in between the two, and SLA increased with precipitation. Thus, different climatic conditions certainly affected the SLA.

Yet, SLA is sensitive to light adaptation. An increase in SLA increases the light contact area of leaves, enhancing the light-catching ability, which in turn, improves both the utilization of light [42] and the photosynthetic capacity of plants. In this study, the SLA of different species was significantly correlated with apparent quantum efficiency (AQY) (Figure 6). The AQY index reflects the ability of plants to absorb, convert, and utilize light energy under low light conditions. The higher the value, the higher the light energy conversion efficiency of leaves. Among the 19 species, *Prunus cerasifera* 'Atropurpurea' was the most adaptable to light, whereas *Pinus tabulaeformis* was the least.

In general, SLA varied greatly with species (50–390 $cm^2 \cdot g^{-1}$). At the regional scale, the distribution range of the SLA of plants in the Beijing Yeya Lake Wetland area was 110–470 $cm^2 \cdot g^{-1}$, and more than half of the plants had a relatively large SLA [43]. This is possibly related to environmental factors. Wetlands have sufficient hydrothermal conditions, and the plant productivity is, thus, relatively high in this habitat. Seventeen species at the Sand Control Station of Shazhuyu in the arid area of Qinghai Province [44] had low SLA, with an average value of 98 $cm^2 \cdot g^{-1}$. The plants in this arid area had a high water conservation ability, which may be a strategic adaptation to water scarcity. The SLA distribution range of the 19 species in this study was 39–238 $cm^2 \cdot g^{-1}$, and for 68.4% of the species it was between 100 and 200 $cm^2 \cdot g^{-1}$. A comparative SLA analysis of plants in different regions and under different natural conditions showed that species in this study area allocated more biomass per unit leaf area and better utilized and preserved environmental and obtained resources, respectively.

The maximum net photosynthetic rate of plants determines their potential photosynthetic capacity. The higher the P_{nmax} value, the higher the carbon sequestration rate, which is beneficial for the accumulation of organic matter [45,46]. In this study, the highest P_{nmax} was of *Amorpha fruticosa* (28.92 $\mu mol \cdot m^2 \cdot s^{-1}$), whereas the lowest was of *Yulania denudata* (6.72 $\mu mol \cdot m^2 \cdot s^{-1}$). This means that *Amorpha fruticosa* had the highest potential photosynthetic capacity and was most able to accumulate organic matter, whereas *Yulania denudata* had the least. Overall, the average P_{nmax} of the 19 species was 17.63 $\mu mol \cdot m^2 \cdot s^{-1}$, which differed from the maximum net photosynthetic rate of plants in other regions. The average P_{nmax} of seven species of curcuma in Guangxi was 6.38 $\mu mol \cdot m^2 \cdot s^{-1}$ [47]. In a study of the net photosynthetic rates of 51 species in an alpine marsh meadow [18], the Pn range was 4.25–19.23 $\mu mol \cdot m^2 \cdot s^{-1}$, with an average of 9.97 $\mu mol \cdot m^2 \cdot s^{-1}$. These results indicate that the growth strategies of these plants differ from those of the Qinglong Lake plantation in Fangshan, which may be related to the semi-humid climate of the latter. However, the P_{nmax} of half of the 97 plant species in Hunshandake Sandy Land, Inner Mongolia was between 10 and 20 $\mu mol \cdot m^2 \cdot s^{-1}$ [48]. For 16 seasonal plants of early spring in the Junggar Desert [49], the P_{nmax} range was 8.07–35.96 $\mu mol \cdot m^2 \cdot s^{-1}$, and the average P_{nmax} was 18.62 $\mu mol \cdot m^2 \cdot s^{-1}$. These results indicate that, although the plant species in Qinglong Lake of Fangshan are in an area with relatively sufficient hydrothermal conditions, their potential photosynthetic capacity is similar to that of plant species in sandy and desert areas. This may be because these species have convergently evolved a similar average P_{nmax} through adaptation to the local environment.

N_{mass} is a key limiting factor of leaf photosynthetic capacity [50]. This is because nitrogen, as the main component of enzymes in plant photosynthesis, is both closely related to photosynthesis [51] and is sensitive to hydrothermal changes. Maximum net photosynthetic rate and N_{mass} were significantly positively correlated (Figure 6), which corroborates greater N_{mass} results in larger photosynthetic capacities of plants [13,40,52,53]. SLA was significantly positively correlated with N_{mass} (Figure 6), which corroborated previous studies [17,44,50]. The smaller the SLA, the smaller the N_{mass}, the smaller the photosynthetic capacity, and the stronger the resistance to stress. N_{mass} significantly differed with plants, and those of *Rhus typhina*, *Ulmus pumila* 'Jinye', and *Amorpha fruticosa* were high (>30 g/kg), resulting in large photosynthetic capacities. However, the N_{mass} of *Pinus bungeana*, *Platycladus orientalis*, and *Pinus tabulaeformis* were low (<15 g/kg), resulting in small photosynthetic capacities.

The average N_{mass} of 1215 plant species from 122 sites (from temperate to tropical, from desert and grassland, to woodland and forest) in the Chinese Plant Characteristics Database [54] was 19.58 g/kg. Globally, from 2883 records in the TRY database [55], the average Pn was 10.3 $\mu mol \cdot m^2 \cdot s^{-1}$, which was lower than 18.62 $\mu mol \cdot m^2 \cdot s^{-1}$ from this study. From 7122 species and 33,880 N_{mass} database records [55], the global average was 17.4 g/kg, which was lower than 21.36 g/kg from this study. The species in this study were more resource-acquiring in nature, and very able in the acquisition of environmental resources.

Plants respond to drought by maximizing the efficiency of their most limited resources, namely WUE, at the expense of NUE and CUE. Plants can also acclimatize to the seasonal occurrence of early spring drought and develop phenotypes with improved WUE [56,57]. Therefore, plant resource utilization efficiency is an indicator of the drought tolerance of a species [25]. High WUE is postulated as beneficial under water-limited conditions. This results in high WUE in drought-tolerant species and low WUE in fast-growing species [58,59]. In contrast, drought-tolerant species are postulated to have low WUE because high WUE is a conservative ecophysiological strategy at the cost of low photosynthetic rate [60]. However, both these opposing views support the conjecture that "differences in WUE between species directly affect their long-term growth and survival in unpredictable and fluctuating conditions in predictable ways" [58]. NUE is an important index of leaf physiology, morphology, and environmental adaptation mechanisms. High NUE denotes high productivity and fast growth rates. CUE is an indicator of leaf carbon balance, and leaves with low CUE have slow tree growth rates and small biomasses [61]. In this study, the conifers *Pinus tabulaeformis* and *Pinus bungeana* had the highest WUE (9.11 and 7.84 $mmol \cdot mol^{-1}$), the highest CUE (94.5% and 85.4%), and the lowest NUE (5.89 and 6.2 $\mu mol \cdot g^{-1} \cdot s^{-1}$). *Euonymus japonicus* 'Aureo-marginatus' and *Prunus cerasifera* 'Atropurpurea' had the lowest WUE (2.54 and 2.91 $mmol \cdot mol^{-1}$), *Euonymus japonicus* 'Aureo-marginatus' and *Platycladus orientalis* had the lowest CUE (71.5% and 76.2%), and *Prunus cerasifera* 'Atropurpurea' had the highest NUE (16.97 $\mu mol \cdot g^{-1} \cdot s^{-1}$). Thus, *Pinus tabulaeformis* and *Pinus bungeana* were highly drought tolerant and highly productive even under drought conditions. *Prunus cerasifera* 'Atropurpurea' had a high resource utilization capacity and fast growth rate. Its large-scale cultivation can improve the productivity of the ecosystem and benefit areas in urgent need of ecological restoration.

4.2. Differences in Leaf Functional Traits and Resource Utilization Efficiency among Life Forms

The richness of plant functional forms is considered a more important ecological indicator than species diversity [18,62,63]. Plants with the same life form are postulated to have either the same or similar leaf traits [64,65]. Therefore, the 19 species in Qinglong Lake in Fangshan were divided into two main categories: trees and shrubs. In general, leaf functional traits and resource utilization significantly differ with life forms. Indeed, conifers (*Pinus tabulaeformis*, *Pinus bungeana*, and *Platycladus orientalis*) and nitrogen-fixing (*Amorpha fruticosa*, *Styphnolobium japonicum*, *Robinia pseudoacacia*) gymnosperms significantly differed from other trees and shrubs (Figure 1). Such differences were reflected in plant life history, morphology, physiology, and other aspects, and were often interpreted as the result of either plant genetic characteristics or environmental adaptations [38]. Considering the vast differences between gymnosperms and nitrogen-fixing plants and other plants, we regrouped the 19 species into four: deciduous trees, deciduous shrubs, evergreen needles, and nitrogen-fixing plants. We found no significant difference between deciduous trees and shrubs. The SLA, P_{nmax}, N_{mass}, and NUE of evergreen conifers were significantly lower than those of deciduous trees and shrubs. The WUE of evergreen conifers was significantly higher than that of other life forms. The SLA, P_{nmax}, and N_{mass} of nitrogen-fixing plants were significantly higher than those of other life forms. Coniferous species had low SLA and tough leaf textures. As plants invest large resources into leaves, they require of them a long service life. Yet, leaf structures still need to ensure the normal physiological and biochemical reactions [66]. Relatedly, the different distribution ratio of leaf nitrogen content between cell wall and photosynthetic systems (Rubisco) affects the growth and survival of plants. The N_{mass} of conifer species was significantly lower than that of deciduous species. Under the influence of intense light and other adverse factors, more nitrogen is allocated to enhance the toughness of plant cell walls and increase the density and thickness of mesophyll cells [66]. Consequently, less nitrogen is allocated to the photosynthetic system [67]. Thus, the P_{nmax} of coniferous trees was significantly lower than that of deciduous trees at similar nutrient input levels. Conifer species are highly adaptable to and highly tolerant of arid environments. However, their low photosynthetic efficiency limits the yield efficiency of assimilated substances. Evergreen and deciduous species have different structural cost investments into unit leaves, such as palisade tissues and thick leaf cell walls [68]. There are four distinct seasons in Beijing, and evergreen plants thus experience environmental stresses such as hot summers, cold winters, intense sunlight, drought, and extreme weather. By increasing investment in leaf structure, plants can reduce SLA and extend the life of leaves to resist the harsh external environment. In this study, the functional traits of nitrogen-fixing plants and conifer species followed completely different adaptation strategies. Nitrogen-fixing plants had the highest SLA, P_{nmax}, and N_{mass}; great light-capturing abilities; high photosynthetic efficiencies; and the highest photosynthetic capacities when resources were abundant.

There were significant differences in WUE and NUE among life forms. The WUE of conifers was significantly higher than that of deciduous trees and shrubs, whereas the NUE of conifers was significantly lower than that of deciduous trees. In this study, the habitat of all tree species was similar, and the differences in resource utilization efficiency were, thus, mainly influenced by genetics. Conifer species improve their competitive advantage under water deficit condition through high WUE. The low WUE and high NUE of deciduous tree species result in the complete absorption of water under adequate supply, resulting in rapid growth and reproduction. By sacrificing the ability to adapt to drought conditions, deciduous tree species improve their competitiveness in resource-rich environments.

The difference in leaf functional traits and resource use efficiency among life forms aid the complete utilization of environmental resources, thus, improving the stability of the entire ecosystem [69,70]. Due to differences in resource strategies, increased coniferous species abundance possibly leads to increased WUE, enhanced drought tolerance, and the decreased photosynthetic production capacity of the entire community. On the contrary, the increased abundance of deciduous plants may increase the P_{nmax} and NUE of the community, resulting in high photosynthetic efficiency that is conducive for biomass recovery.

4.3. Correlations between Leaf Functional Traits and Resource Use Efficiency

4.3.1. Correlations between Resource Utilization Efficiency

Plant maximization of carbon uptake or use efficiency theories depend on trade-offs of resource use efficiency. According to the eco-economic theory, plants maximize the utilization efficiency of the most limited resources by reducing the utilization efficiency of abundant resources [24]. The trade-off between WUE and NUE is known; plants cannot concurrently maximize both NUE and WUE [25,71–73], and this is mainly determined by the physiological characteristics of leaves. Nitrogen affects photosynthesis, water affects transpiration, and stomatal behavior controls both photosynthesis and transpiration [74,75]. Since the intercellular CO_2 concentration (C_i) of leaves is usually not saturated for carbon assimilation, an increase in stomatal conductance increases C_i, leading to increased plant photosynthetic rates and NUE. Transpiration is also enhanced, resulting in increased water loss, and thus, decreased WUE [71,72]. In their studies on dominant plants in the arid steppe of Inner Mongolia, Gong et al. also pointed out that NUE decreased when plants maximized the WUE [27]. Relatedly, NUE was significantly negatively correlated with WUE in coniferous mixed forests [76], which is consistent with this theory. These findings were from arid and semi-arid areas, yet they were corroborated by our study of a subhumid plantation area where NUE was also significantly negatively correlated with WUE. WUE and CUE were significantly positively correlated, i.e., an increase in NUE resulted in a decrease in plant water and carbon use efficiency. This may be due to the subhumid climate of the study area, which results in abundant water supply, and thus, increased NUE. Therefore, to better understand the strategies of plant resource utilization in the subhumid plantation area, it is important to continually study changes in leaf nitrogen content and distribution ratio.

4.3.2. Correlations between Leaf Functional Traits and Resource Use Efficiency

In leaves, plant resource use efficiency changed with functional traits, especially N_{mass}, SLA, and P_{nmax}. The first two parameters predict the WUE [27]. In this study, WUE was significantly negatively correlated with N_{mass} and SLA, which corroborates previous studies. However, there was no significant relationship between WUE and P_{nmax}, possibly because changes in the allocated biomass by leaves per unit caused both corresponding changes in photosynthetic capacity and affected transpiration. CUE and NUE were positively correlated with P_{nmax}. Leaf CUE, as an important indicator of leaf carbon balance, results from the comprehensive effects of photosynthesis and respiration [61]. In this study, P_{nmax} was positively correlated with R_d, and CUE was negatively correlated with R_d. This indicated a large increase in R_d, probably because respiration is more susceptible to changes than photosynthesis [13,61]. The extremely significant positive correlation between NUE and P_{nmax} ($p < 0.001$) was consistent with a previous study [66] and confirmed that the greater the allocation of photosynthetic nitrogen to the Rubisco enzyme, the higher the photosynthetic rate and production capacity. These findings indicate that the functional traits of plants represent their utilization of and adaptation to environmental resources.

5. Conclusions

In this study, 19 plant species growing in the 10,000 mu plantation park of Qinglong Lake in Fangshan were investigated. First, leaf functional traits and resource utilization characteristics significantly differed among the plant species. This indicated that, to fully acquire and use environmental resources, different plants adapt to the same environment in different ways. Second, the significant differences in these indexes among life forms may be related to their life history and resource utilization strategies. Evergreen conifers and deciduous species each represented plant adaptive strategies. Such insights aid the selection of ideal restoration species for plantations in different regions and under different environmental conditions, according to the resource utilization characteristics of different life forms. Third, there was a strong correlation both between different plant resource use efficiencies and between leaf functional traits and resource use efficiency. This indicated synergistic changes between leaf functional traits and resource use efficiency in different species, suggesting that resource use changes can be predicted by leaf functional traits. In the future, we will deeply discuss the impact of these changes on the stability of the entire community and even the ecosystem.

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References

1. Reich, P.B.; Cornelissen, H. The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *J. Ecol.* **2014**, *102*, 275–301. [CrossRef]
2. Anderegg, L.D.L.; Berner, L.T.; Badgley, G.; Sethi, M.L.; Law, B.E.; Hille Ris Lambers, J. Within-species patterns challenge our understanding of the leaf economics spectrum. *Ecol. Lett.* **2018**, *21*, 734–744. [CrossRef]
3. Sun, M.; Tian, K.; Zhang, Y.; Wang, H.; Guan, D.X.; Yue, H.T. Research on leaf functional traits and their environmental adaptation. *Plant Sci. J.* **2017**, *35*, 940–949.
4. Petrik, P.; Peter-Petrik, A.; Kurjak, D.; Mukarram, M.; Klein, T.; Gömöry, D.; Střelcová, K.; Frýdl, J.; Konôpková, A. Interannual adjustments in stomatal and leaf morphologicaltraits of European beech (*Fagus sylvatica* L.) demonstrate itsclimate change acclimation potential. *Plant Biol.* **2022**, *24*, 1287–1296. [CrossRef]
5. Webb, C. Exploring the Phylogenetic Structure of Ecological Communities: An Example for Rain Forest Trees. *Am. Nat.* **2000**, *156*, 145–155. [CrossRef]
6. Yao, T.T.; Meng, T.T.; Ni, J.; Yan, S.; Feng, X.H.; Wang, G.H. Leaf functional trait variation and its relationship with plant phylogenic background and the climate in Xinjiang Junggar Basin, NW China. *Biodivers. Sci.* **2010**, *18*, 188–198.
7. Xu, Y.D.; Dong, S.K.; Li, S.; Shen, H. Research progress on ecological filtering mechanisms for plant community assembly. *Acta Ecol. Sin.* **2019**, *39*, 2267–2281.
8. Liu, J.H.; Zeng, D.H.; Lee, D.K. Leaf traits and their interrelationships of main plant species in southeast Horqin sandy land. *Chin. J. Ecol.* **2006**, *25*, 921–925.
9. Wang, R.L.; Yu, G.R.; He, N.P.; Wang, Q.F.; Zhao, N.; Xu, Z.W. Latitudinal variation of leaf morphological traits from species to communities along a forest transect in eastern China. *J. Geogr. Sci.* **2016**, *26*, 15–26. [CrossRef]
10. Sultan, S.E. Evolutionary Implications of Phenotypic Plasticity in Plants. *Evol. Biol.* **1987**, *138*, 213–223.
11. Smith, E.C.; Griffiths, H.; Wood, L.; Gillon, J. Intra-specific variation in the photosynthetic responses of cyanobiont lichens from contrasting habitats. *New Phytol.* **1998**, *138*, 213–224. [CrossRef]
12. Ackerly, D.D.; Dudley, S.A.; Sultan, S.E.; Schmitt, J.; Coleman, J.S.; Linder, C.R.; Sandquist, D.R.; Geber, M.A.; Evans, A.S.; Dawson, T.E.; et al. The Evolution of Plant Ecophysiological Traits: Recent Advances and Future Directions. *BioScience* **2000**, *50*, 979–995. [CrossRef]
13. Wright, I.J.; Reich, P.B.; Westoby, M.; Ackerly, D.D.; Baruch, Z.; Bongers, F.; Cavender-Bares, J.; Chapin, T.; Cornelissen, J.H.C.; Diemer, M.; et al. The worldwide leaf economics spectrum. *Nature* **2004**, *428*, 821–827. [CrossRef]
14. Meng, T.T.; Ni, J.; Wang, G.H. Plant functional traits, environments and ecosystem functioning. *Chin. J. Plant Ecol.* **2007**, *31*, 150–165.
15. Wang, M.J.; Rong, L.; Li, T.T.; Wang, Q.; Ye, T.M. Studies on leaf functional traits of nine woody lianas in the Karst area of central Guizhou province. *J. Trop. Subtrop. Bot.* **2021**, *29*, 455–464.
16. Wang, Z.Q.; Huang, H.; Wang, H.; Peñuelas, J.; Sardans, J.; Niinemets, Ü.; Niklas, K.J.; Li, Y.; Xie, J.B.; Wright, L.J. Leaf water content contributes to global leaf trait relationships. *Nat. Commun.* **2022**, *13*, 5525. [CrossRef]
17. Li, H.L.; Xu, D.H.; Du, G.Z. Effect of change of plant community composition along degradation gradients on water conditions in an alpine swamp wetland on the Qinghai-Tibetan Plateau of China. *Chin. J. Plant Ecol.* **2012**, *36*, 403–410. [CrossRef]
18. Ren, Q.J.; Li, H.L.; Bu, H.Y. Comparison of physiological and leaf morphological traits for photosynthesis of the 51 plant species in the Maqu alpine swamp meadow. *Chin. J. Plant Ecol.* **2015**, *39*, 593–603.
19. Grime, J.P. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. *Am. Nat.* **1977**, *111*, 1169–1194. [CrossRef]
20. Hatfield, J.L.; Dold, C. Water-Use Efficiency: Advances and Challenges in a Changing Climate. *Front. Plant Sci.* **2019**, *10*, 103. [CrossRef]
21. Gifford, R.M. Plant respiration in productivity models: Conceptualisation, representation and issues for global terrestrial carbon-cycle research. *Funct. Plant Biol.* **2003**, *30*, 171–186. [CrossRef] [PubMed]
22. Luo, Y.; Su, B.; Currie, W.; Dukes, J.; Finzi, A.; Hartwig, U.; Hungate, B.; McMurtrie, R.; Oren, R.; Parton, W.; et al. Progressive Nitrogen Limitation of Ecosystem Responses to Rising Atmospheric Carbon Dioxide. *BioScience* **2004**, *54*, 731–739. [CrossRef]
23. Wang, Q.W.; Yu, D.P.; Dai, L.M.; Zhou, L.; Zhou, W.M.; Qi, G.; Qi, L.; Ye, Y.J. Research progress in water use efficiency of plants under global climate change. *Chin. J. Appl. Ecol.* **2010**, *21*, 3255–3265.
24. Bloom, A.J.; Chapin, F.S.; Mooney, H.A. Resource Limitation in Plants-An Economic Analogy. *Ann. Rev. Ecol. System.* **1985**, *16*, 363–392. [CrossRef]
25. Limousin, J.M.; Yepez, E.A.; McDowell, N.G.; Pockman, W.T.; Tjoelker, M. Convergence in resource use efficiency across trees with differing hydraulic strategies in response to ecosystem precipitation manipulation. *Funct. Ecol.* **2015**, *29*, 1125–1136. [CrossRef]

26. Szatniewska, J.; Zavadilova, I.; Nezval, O.; Krejza, J.; Petrik, P.; Cater, M.; Stojanovic, M. Species-specific growth and transpiration response to changing environmental conditions in floodplain forest. *For. Ecol. Manag.* **2022**, *516*, 120248. [CrossRef]
27. Gong, X.Y.; Chen, Q.; Lin, S.; Brueck, H.; Dittert, K.; Taube, F.; Schnyder, H. Tradeoffs between nitrogen- and water-use efficiency in dominant species of the semiarid steppe of Inner Mongolia. *Plant Soil* **2011**, *340*, 227–238. [CrossRef]
28. Loreau, M. Biodiversity and ecosystem functioning: Recent theoretical advances. *Oikos* **2000**, *91*, 3–17. [CrossRef]
29. Loreau, M.; Hector, A. Partitioning selection and complementarity in biodiversity experiments. *Nature* **2001**, *412*, 72–76. [CrossRef]
30. Li, X.H.; Yan, H.J.; Wei, T.Z.; Zhou, W.J.; Jia, X.; Zha, T.S. Relative changes of resource use efficiencies and their responses to environmental factors in Artemisia ordosica during growing season. *Chin. J. Plant Ecol.* **2019**, *43*, 889–898. [CrossRef]
31. Zhou, W.J.; Zha, T.S.; Jia, X.; Tian, Y.; Wei, T.Z.; Jin, C. Dynamics of water use efficiency of Artemisia ordosica leaf in growing season in response to environmental factors in Yanchi, Ningxia of northwestern China. *J. Beijing For. Univ.* **2020**, *42*, 98–105.
32. Jiang, Y.; Jin, C.; Jiang, X.Y.; Li, X.H.; Wei, N.N.; Gao, S.J.; Liu, P.; Jia, X.; Zha, T.S. Relative changes and biophysical controls of leaf resource use efficiencies in Artemisia ordosica. *Acta Ecol. Sin.* **2022**, *42*, 15.
33. Hu, L.D.; Zhou, H.J.; Huang, Y.Z.; Yao, X.Y.; Ye, S.M.; Yu, S.F. A study on plant species diversity and soil carbon and nitrogen in different Cunninghamia lanceolata stand types. *Ecol. Environ. Sci.* **2022**, *31*, 451–459.
34. Cao, S. Excessive reliance on afforestation in China's arid and semi-arid regions: Lessons in ecological restoration. *Earth Sci. Rev.* **2011**, *104*, 240–245. [CrossRef]
35. Ye, Z.P.; Yu, Q.; Kang, H.J. Evaluation of photosynthetic electron flow using simultaneous measurements of gas exchange and chlorophyll fluorescenceunder photorespiratory conditions. *Photosynthetica* **2012**, *50*, 472–476. [CrossRef]
36. Li, X.Q.; Lu, Y.M.; Huang, A.M.; Yuan, R.B.; Li, J.L.; Hu, D.D.; Zhong, Q.L.; Cheng, D.L. Light response model fitting and photosynthetic characteristics of tendifferent fern species in subtropics. *Acta Ecol. Sin.* **2022**, *42*, 3333–3344.
37. Jiang, G.M.; He, W.M. Species-and habitat-variability of photosynthesis transpiration and water use efficiency of different plant species in Maowusu sand area. *Chin. J. Plant Ecol.* **1999**, *41*, 1114–1124.
38. Zhao, H.Y.; Li, Y.L.; Wang, X.Y.; Mao, W.; Zhao, X.Y.; Zhang, T.H. Study on the variation of leaf characters of 52 species of plants in Horqin sandy land. *J. Desert Res.* **2010**, *30*, 1292–1298.
39. Li, Y.L.; Cui, J.Y.; Su, Y.Z. Specific leaf area and leaf dry matter content of some plants in different dune habitats. *Acta Ecol. Sin.* **2005**, *25*, 304–311.
40. Lv, J.Z.; Miao, Y.M.; Zhang, H.F.; Bi, R.C. Comparisons of leaf traits among differernt functional types of plant from Huoshan mountain in the Shanxi province. *J. Wuhan Botan. Res.* **2010**, *28*, 460–465.
41. Zhang, Z.G.; Wei, H.X. Specific Leaf Area and Leaf Dry Matter Content of Main Plant Species in Red Lotus Wetland of Weishan Lake. *Acta Agric. Jiangxi* **2021**, *33*, 63–69.
42. Yang, Q.; Chen, Z.F.; Zhou, J.J.; Lai, S.B.; Jian, C.X.; Wang, Z.; Xu, B.C. Responses of leaf functional traits of dominant plant species in grassland communities to nitrogen and phosphorus addition in loess hilly—Gully region. *Chin. J. Appl. Ecol.* **2019**, *30*, 3697–3706.
43. Liu, X.X.; Li, J.Q. Study on the functional traits of plant leaf in Beijing yeyahu wetland. *J. Anhui Agric.* **2008**, *36*, 8046–8409, 8428.
44. Li, Y.H.; Luo, T.X.; Lu, Q.; Tian, X.Y.; Wu, B.; Yang, H.H. Comparisons of leaf traits among 17major plant species in Shazhuyu Sand Control Experimental Station of Qinghai Province. *Acta Ecol. Sin.* **2005**, *25*, 994–999.
45. Mahmud, K.; Medlyn, B.E.; Duursma, R.A.; Company, C.; DeKauwe, M.G. Inferring the effects of sink strength on plant carbon balance processes from experimental measurements. *Biogeosciences* **2018**, *15*, 4003–4018. [CrossRef]
46. Vona, V.; Di Martino Rigano, V.; Andreoli, C.; Lobosco, O.; Caiazzo, M.; Martello, A.; Carfagna, S.; Salbitani, G.; Rigano, C. Comparative analysis of photosynthetic and respiratory parameters in the psychrophilic unicellular green alga Koliella antarctica, cultured in indoor and outdoor photo-bioreactors. *Physiol. Mol. Biol. Plants* **2018**, *24*, 1139–1146. [CrossRef] [PubMed]
47. Li, Y.; Peng, Y.D.; Yu, L.Y.; Chen, X.Y.; Pan, C.L.; Lan, Z.Z.; Huang, X.Y. Study on Photosynthetic Characteristics of several Curcuma plants. *Jiangsu Agric. Sci.* **2021**, *49*, 143–149.
48. Niu, S.L.; Jiang, G.M.; Gao, L.M.; Li, Y.G.; Liu, M.Z. Comparison of gas exchange traits of differernt plant species in hunshandak sand area. *Chin. J. Plant Ecol.* **2003**, *27*, 318–324.
49. Qiu, J.; Tan, D.Y.; Fan, D.Y. Characteristics of photosynthesis and biomiss allocation of spring ephemerals in the junggar desert. *Chin. J. Plant Ecol.* **2007**, *31*, 883–891.
50. Li, X.R.; Liu, Q.J.; Cai, Z.; Ma, Z.Q. Specific leaf area and leaf area index of conifer plantations in Qianyanzhou station of subtropical China. *Chin. J. Plant Ecol.* **2007**, *31*, 93–101.
51. Chen, Z.H.; Zha, T.S.; Jia, X.; Wu, Y.; Wu, B.; Zhang, Y.; Guo, J.; Qin, S.; Chen, G.; Peltola, H. Leaf nitrogen is closely coupled to phenophases in a desert shrub ecosystem in China. *J. Arid Environ.* **2015**, *122*, 124–131. [CrossRef]
52. Takashima, T.; Hikosaka, K. Photosynthesis or persistence: Nitrogen allocation in leaves of evergreen and deciduous Quercus species. *Plant Cell Environ.* **2004**, *27*, 1047–1054. [CrossRef]
53. Yu, H.Y.; Chen, Y.T.; Xu, Z.Z.; Zhou, G.S. Analysis of relationships among leaf functional traits and economics spectrum of plant species in the desert steppe of Nei Mongol. *Chin. J. Plant Ecol.* **2014**, *38*, 1029–1040.
54. Zhang, X.; He, X.; Gao, J.; Wang, L. Latitudinal and climate effects on key plant traits in Chinese forest ecosystems. *Glob. Ecol. Conserv.* **2019**, *17*, e00527. [CrossRef]
55. Kattge, J.; Diaz, S.; Lavorel, S.; Prentice, C.; Leadley, P.; Bonisch, G.; Garnier, E.; Westoby, M.; Reich, P.B.; Wright, I.J.; et al. TRY—A global database of plant traits. *Glob. Chang. Biol.* **2011**, *17*, 2905–2935. [CrossRef]

56. Petrik, P.; Peter-Petrik, A.; Konôpková, A.; Fleischer, P.; Stojnic, S.; Zavadilova1, I.; Kurjak, D. Seasonality of PSII thermostability and water use efciency of in situ mountainous Norway spruce (*Picea abies*). *J. For. Res.* **2022**, 1–12.
57. Guerrieri, R.; Belmecheri, S.; Ollinger, S.V.; Asbjornsen, H.; Jennings, K.; Xiao, J.; Stocker, B.D.; Martin, M.; Hollinger, D.Y.; Bracho-Garrillo, R.; et al. Disentangling the role of photosynthesis and stomatalconductance on rising forest water-use efficiency. *Proc. Natl. Acad. Sci. USA* **2019**, *116*, 16909–16914. [CrossRef]
58. Ehleringer, J.R.; Cooper, T.A. Correlations between carbon isotope ratio and microhabitat in desert plants. *Oecologia* **1988**, *76*, 562–566. [CrossRef]
59. Fischer, R.A.; Turner, N.C. Plant productivity in the arid and semiarid zones. *Annu. Rev. Plant Physiol.* **1978**, *29*, 277–317. [CrossRef]
60. Miller, J.M.; Williams, R.J.; Farquhar, G.D. Carbon isotope discrimination by a sequence of Eucalyptus species along a subcontinental rainfall gradient in Australia. *Funct. Ecol.* **2001**, *15*, 222–232. [CrossRef]
61. Quan, X.Q.; Wang, C.K. Adaptation of leaf carbon use efficiency of Larix gmelinii to environmental change. *Acta Ecol. Sin.* **2016**, *36*, 3381–3390.
62. Tilman, D.; Knops, J.; Wedin, D.; Reich, P.; Ritchie, M.; Siemann, E. The Influence of Functional Diversity and Composition on Ecosystem Processes. *Am. Assoc. Adv. Sci.* **1997**, *277*, 1300–1302. [CrossRef]
63. Mack, M.C.; D'Antonio, C.M. Impacts of biological invasions on disturbance regimes. *Trends Ecol. Evol.* **1998**, *13*, 195–198. [CrossRef] [PubMed]
64. Lauenroth, W.K.; Dodd, J.L. The Effects of Water- and Nitrogen-Induced Stresses on Plant Community Structure in a Semiarid Grassland. *Oecologia* **1978**, *36*, 211–222. [CrossRef] [PubMed]
65. Monica, L.P.; Roger, L.S.; Catherine, A.Z.; Richard, E.E.; Tony, J.S.; Borkowski, J.J. Plant Functional Group Diversity as a Mechanism for Invasion Resistance. *Restor. Ecol.* **2005**, *13*, 448–459.
66. Zheng, S.X.; ShangGuan, Z.P. Photosynthetic characteristics and their relationships with leaf nitrogen content and leaf mass per area in different plant functionaltypes. *Acta Ecol. Sin.* **2007**, *27*, 171–181.
67. Onoda, Y.; Hikosaka, K.; Hirose, T. Allocation of Nitrogen to Cell Walls Decreases Photosynthetic Nitrogen-Use Efficiency. *Funct. Ecol.* **2004**, *18*, 419–425. [CrossRef]
68. Huang, W.J.; Li, Z.J.; Yang, Z.P.; Bai, G.Z. The structural traits of populus euphratica heterom orphic leaves and their correlations. *Acta Ecol. Sin.* **2010**, *30*, 4636–4642.
69. Shahid, N.; Lindsey, J.T.; Sharon, P.L.; John, H.L.; Woodfin, R.M. Declining biodiversity can alter the performance of ecosystems. *Nature* **1994**, *368*, 734–737.
70. Anderson, J.E.; Inouye, R.S. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecol. Monogr.* **2001**, *71*, 531–556. [CrossRef]
71. Patterson, T.B.; Guy, R.D.; Dang, Q.L. Whole-plant nitrogen- and water-relations traits, and their associated trade-offs, in adjacent muskeg and upland boreal spruce species. *Oecologia* **1997**, *110*, 160–168. [CrossRef] [PubMed]
72. Chen, S.; Bai, Y.; Zhang, L.; Han, X. Comparing physiological responses of two dominant grass species to nitrogen addition in Xilin River Basin of China. *Environ. Exp. Bot.* **2005**, *53*, 65–75. [CrossRef]
73. Wang, G.H. Can the restoration of natural vegetation be accelerated on the Chinese Loess Plateau? A study of the response of the leaf carbon isotope ratio of dominant species to changing soil carbon and nitrogen levels. *Ecol. Res.* **2005**, *21*, 188–196. [CrossRef]
74. Yuan, Z.Y.; Li, L.H. Soil water status influences plant nitrogen use: A case study. *Plant Soil* **2007**, *301*, 303–313. [CrossRef]
75. Zhan, X.Y.; Yu, G.R.; Sheng, W.P.; Fang, H.J. Foliar water use efficiency and nitrogen use efficiency of dominant plant species in main forests along the North-South Transect of East China. *Chin. J. Appl. Ecol.* **2012**, *23*, 587–594.
76. Tarvainen, L.; Rantfors, M.; Wallin, G. Seasonal and within-canopy variation in shoot-scale resource-use efficiency trade-offs in a Norway spruce stand. *Plant Cell Environ.* **2015**, *38*, 2487–2496. [CrossRef]