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Competition and Plant Trait Plasticity of Invasive (*Wedelia trilobata*) and Native Species (*Wedelia chinensis*, WC) under Nitrogen Enrichment and Flooding Condition

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Abstract: Nitrogen (N) is the important nutrition that regulatory plant functioning and environmental stability of invasive plant species under flooding (F) conditions. Little information clarifies the role of nitrogen enrichment and flooding on the invasive plant functional traits and competition with native competitors. Plant functional traits play an essential role in the successful growth of plants under different environmental conditions. Therefore, greenhouse pots experiment was conducted with invasive plant species (*Wedelia trilobata*, WT), and its native competitor (*Wedelia chinensis*, WC) in monoculture and cocultivation culture, along with flooding and nitrogen enrichment conditions. Considering the impact of flooding (F) and nitrogen (N) on an individual basis, the plant physiological traits of WC were nonsignificant compared to that of WT. However, in the combination of flooding × additional nitrogen (F.N, F.2N), plant physiological traits of WT were comparatively higher than those of WC, especially in cocultivation. In flooding × additional nitrogen (F.N and F.2N), better phenotypic plasticity at different plant traits makes WT more dominant in resource competition over WC. In conclusion, improved functional traits of WT under nitrogen enrichment and flooding conditions enhanced its competitiveness over native competitors.

Keywords: phenotypic plasticity; resources variations; flooding; invasive plant species; plant interaction; wetland

Citation: Azeem, A.; Wenxuan, M.; Changyan, T.; Javed, Q.; Abbas, A. Competition and Plant Trait Plasticity of Invasive (*Wedelia trilobata*) and Native Species (*Wedelia chinensis*, WC) under Nitrogen Enrichment and Flooding Condition. *Water* **2021**, *13*, 3472. https://doi.org/10.3390/w13233472

Academic Editor: Jesus Gonzalez-Lopez

Received: 23 October 2021
Accepted: 22 November 2021
Published: 6 December 2021

1. Introduction

Invasive plant species pose a severe threat to the native ecosystems and cause considerable losses to the world economy [1]. Global climate change and environmental disturbance could create better resources for invasive plant species to grow [2]. Several experimental studies described environmental disturbance enhanced plant invasion. For instance, a recent meta-analysis comparing the growth performance of 74 invasive and 117 native plant species in response to global environmental changes, i.e., flooding, nitrogen enrichment, and temperature variations, noted that these changes could help invasive plant species to grow faster [3]. Functional traits play a significant role in the successful invasion of invasive plant species over native plant species under these global environmental changes [4]. Functional traits response under different environmental factors such as nutrient availability, temperature variations, and water fluctuation also give a brief understanding of the success of invasive plant species in the native ecosystems [5].

Nevertheless, it is interesting to recognize functional traits that boost invasive plant species growth over native competitors. Functional traits such as growth characteristics are key indicators of the root, shoot development. Leaf functional traits are also crucial indicators of transpiration, evaporation, and photosynthesis [6].

According to the resource ratio hypothesis, invasive plant species vary their nutrients and water requirements, which helps them to cope with different environmental conditions [7]. Invasive plant species show strong responses under these disturbed environmental conditions and capture the resources to reduce the growth of their native competitor [8]. Invasive plant species show better functional traits under nutrient enrichment and water fluctuations because of higher phenotypic plasticity and better competition intensity of interspecies [9]. Relative competition intensity and phenotypic plasticity seem to benefit plants to cope with these environmental changes and capture resources by destroying the growth of their native competitor [10,11].

Mostly competitive ability of invasive and native plant species depends on the resources of the habitats. Invasive plant species like to grow in resource-rich habitats. Thus, the competition ability of invasive plant species may alter with the availability of resources. There are numerous examples that variation in resources affects the performance of invasive plant species. For example, nitrogen (N) enrichment enhanced invasion of *Berberis thunbergii, Wedelia trilobata* [12], *Robinia pseudoacacia*, and competitive ability of *Centaurea stoebe* [2] potassium addition made *Taraxacum officinale* more effective in grassland [13]. Several nutrients played a role in the success of invasive plant species, but N is a major element of global change that disturbs plant community structure. Nitrogen enrichment enhances the abundance of invasive plant species and decreases the native plant species richness [14]. Nitrogen enrichment plays the main role in the spread of invasive plant species. Nitrogen enrichment changed soil properties that favor invasive plant species to grow faster and capture the resources [15].

Water fluctuation is a key indicator of hydrological regimes responsible for shaping plant communities in wetlands [16,17]. Frequent water fluctuations make a greater impact on the availability of resources such as light, CO_2, O_2, and nutrients [18,19]. In water fluctuation, flooding conditions make or invasive plant species favorable because they use "escape or quiescence" techniques to cope with flooding for better growth [20]. Flooding can be observed as a disturbance to the plant community. It creates resources-rich habitats that facilitate the invasion of invasive plant species over native [21]. Water availability is not enough for the successful invasion of invasive plant species because they like to grow in nutrients-water rich habitats [22]. Flooding with nitrogen enrichment has a great influence on the successful invasion of invasive plant species. Therefore, the response of the functional traits of invasive plant species under nitrogen enrichment and flooding conditions allows us to manage the growth of invasive plant species under these environmental conditions. For this purpose, we experimented to examine the functional traits of the invasive plant species *Wedelia trilobata* and its congener native *Wedelia chinensis* under nitrogen enrichment, flooding, and their interaction, in different plant cultures. We hypothesized that flooding and additional nitrogen concentration enhance the success of invasive plant species over native plant species due to better physiological and growth responses of functional traits. In this study, we addressed the following objectives: (1) "How does the nitrogen enrichment along with flooding affect functional traits of an invasive plant and its native congener?" and (2) do the resources-rich conditions, such as nitrogen enrichment and flooding, make the invasive species competitively superior to its native congener?

2. Materials and Methods

This study was conducted from April to July 2019 under greenhouse conditions having a temperature of 25 ± 5 °C with 60% relative humidity and no artificial light. The greenhouse is located at Jiangsu University, Zhenjiang, China (32.20° N, 119.45° E). Wedelia trilobata (WT) is an annual invasive plant species in China [2], while Wedelia chinensis (WC) is its congener native species belonging to the Asteraceae family; both were chosen in this study [2]. Wedelia trilobata is native to Mexico, Central America, and Caribbean. It was introduced all over the world in a semiarid, arid, and humid region [23]. In China, it was initially introduced as a groundcover species but later spread rapidly from gardens to roadsides, and then to the agricultural fields. Nowadays, it is found near the riverside as well [24,25]. WC is the native congener of WT. It is mostly used as a medicinal plant.

WT was mostly found in humid regions of China like Yangzhou and Guangzhou. Some of the populations of WT were also found near the Yangzi River in Jiangsu province of China. This probably indicates that water fluctuation and nutrient enrichment made WT successful in these environments. Ramets of WT and WC were collected from the single location of Jiangsu University for the experiment. Ramets of WT and WC were grown in the seedling trays with sand as the growing medium. These trays were placed in a greenhouse. The ramets were irrigated with distilled water every day, while nutrition was provided weekly through Hoagland solution. When ramets had four fully expanded leaves, then these were transferred to plastic pots (height = 10 cm, diameter = 13 cm) containing sand as a growing-medium. The average height and dry weight of ramets were recorded at the time of transplanting, which was, respectively, 10.10 cm and 0.095 g for WT, and 8.50 cm and 0.075 g for WC. The ramets in the pots were placed in the greenhouse for one week to let them maintain their growth within the pots. The two plant species were left growing under two cultures, i.e., monoculture and cocultivation. In monoculture, two plants of each species grew; in cocultivation, one plant of WT and WC grew together. Subsequently, the treatments were implemented as three levels of nitrogen (control = 0.043 g, denoted as CK; additional = 0.130 g, denoted as N and double additional = 0.261 g, denoted as 2N) and two levels of water (normal water = 0.450 L/week and flooding = 0.9 L/week) (Figure 1). Nitrogen treatments prepared according to [4] comprised of equal proportions of KNO_3 and NH_4Cl. Water treatments were made according to the procedure outlined by [17]. Nitrogen treatments were renewed once a week. The required water amount for water treatments was given three times a week. Two environmental factors were subjected to all pots after transplanting based on factorial design: water (normal or flooding), nitrogen (control, additional, or double additional), and three cultures (two monoculture and one cocultivation), with five replicates. According to this experimental design, there were 90 pots (3 nitrogen levels × 2 water levels × 3 cultures × 5 replicates).

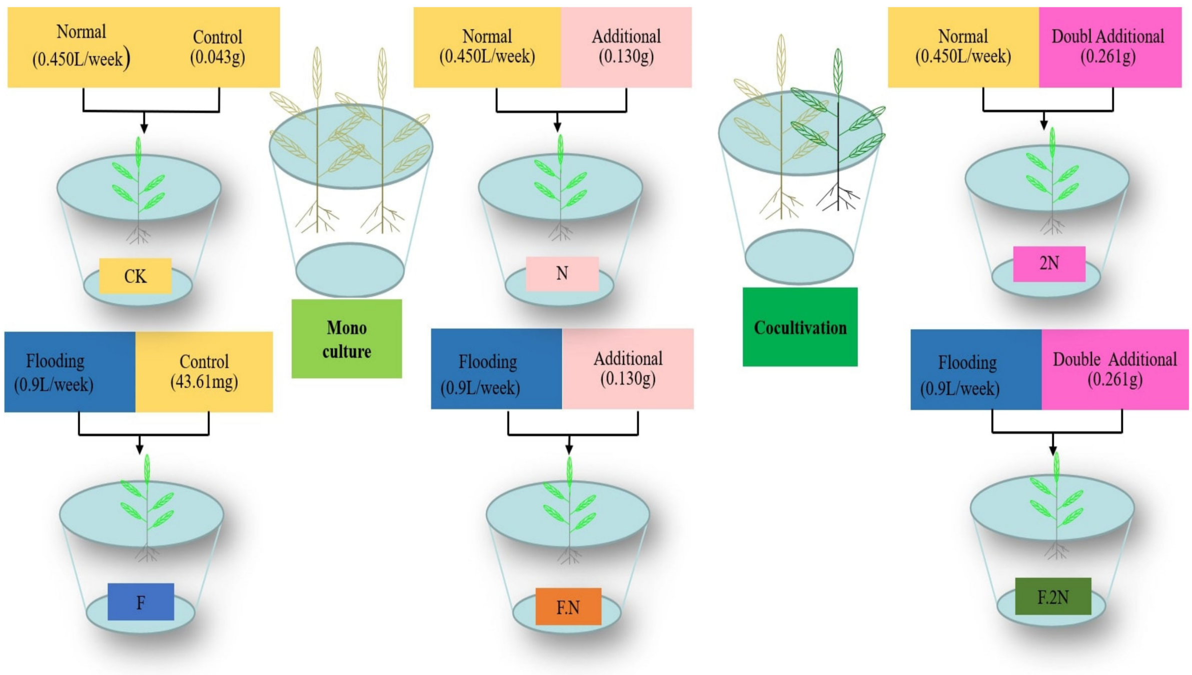

Figure 1. Details of experimental treatments and their combination along with planting culture. Nitrogen treatments were made with an equal proportion of KNO_3 and NH_4Cl. Note: F = combination of water flooding along with control nitrogen, CK = normal water along with control nitrogen, F.N = flooding along with additional nitrogen, N = normal water along with additional nitrogen, F.2N = flooding along with additional double nitrogen, 2N = normal water along with additional double nitrogen.

2.1. Growth and Physiological Traits Measurement

Two months after the treatment, i.e., in July, leaf nitrogen of both species was measured with a hand-held plant nutrient meter (TYS-3N, TOP Instrument Co., Ltd., Hangzhou, China). Whereas leaf chlorophyll content (CHI) was measured with a portable chlorophyll meter, SPAD; Oakoch OK-Y104, China.

Leaf area was measured with ImageJ software for every individual plant with five replicates. The plant height of every individual plant with five replicates was measured with a measuring scale. After harvesting, plants were carefully washed with water to remove sand particles. Separate above ground (leaf and stem) biomass and below ground (root) biomass of each individual. These samples were put into oven at 72 °C for 48 h to measure dry weight of each individual [26]. The relative growth rate of total dry weight (RGR_B), relative growth rate of stem length (RGR_{SL}), stem weight ratio (SWR), root weight ratio (RWR) and leaf specific area (SLA) were calculated using the following equations shown in Table 1.

Table 1. Equations to measure different growth traits.

Traits (Abbreviation)	Equation	Units	Note
Relative growth rate of total dry weight (RGR_B)	$RGR_B = \frac{(lnBM_f - lnBM_i)}{t}$	g/day	BM and Sl represent total dry weight and stem length respectively. t means total time for experiment, and f and i represented final and initial values respectively.
Relative growth rate of stem length (RGR_{Sl})	$RGR_{Sl} = \frac{(lnSl_f - lnSl_i)}{t}$	cm/day	
Stem weight ratio (SWR)	$SWR = \frac{\text{Total stem weight}}{\text{total weight}}$	g/g	
Root weight ratio (RWR)	$RWR = \frac{\text{Total root weight}}{\text{total weight}}$	g/g	
Specific leaf area (SLA)	$SLA = \frac{\text{Leaf area}}{\text{Leaf dry weight}}$	mm^2/mg	

The relative competition intensity (RCI) of different functional traits was calculated by using below equation [13,27] between WT and WC under different nitrogen and water treatments.

$$RCI = (A\_mix - A\_mono)/(A\_mix + A\_mono) \tag{1}$$

A_mix is the trait value of either WT or WC in the cocultivation, while Amono is the trait value of either WT or WC in the monoculture. RCI values range from −1 to 1. Negative values indicate competition; positive values indicate facilitation; and a 0 value means neither competitive nor facilitative interactions.

The phenotypic plasticity index (P_I) of functional traits was calculated by using below equation [28,29], to determine the range of phenotypic plasticity of different functional traits of WT and WC under different nitrogen and water treatments within cocultivation.

$$P\ (\text{Maximum value} - \text{Minimum value})/(\text{Maximum value}) \tag{2}$$

2.2. Statistical Analysis

Assumptions of parametric statistics were tested to verify normality and homogeneity of variance using the Shapiro–Wilk normality test and Levene's test before further analysis. Three-way ANOVA, along with water, nitrogen, and plant culture as a main factor, was performed to determine the main effects and interaction effects on each functional trait ($p \leq 0.05$). Furthermore, a posthoc Tukey test, $p < 0.05$, was used for multiple comparison to measure the significant different between the treatments. Pearson Correlation of the traits' mechanisms (RGR_B, RGR_{SL}, SWR, RWR) between both species within monoculture under each treatment can be determined (Hodgins et al., 2015). All analyses were conducted in SPSS:22, and graphs were made in the software Origin Pro9.

3. Results

3.1. Functional Traits

The individual effect of water (W), nitrogen (N), culture (C), and their interactions (W × N × C) affected the functional traits ($p < 0.01$, Table 2). CHI, was nonsignificant by the interaction of W × N, and SLA was nonsignificant by the interaction of W × C. Plant height, and leaf nitrogen was not affected by C. The remaining other functional traits were affected significantly by each individual factor and their interaction ($p < 0.01$, 0.05; Table 2). Plant height of WT and WC under flooding (F), nitrogen (N), and additional nitrogen (2N) were nonsignificant under monoculture but significant under cocultivation. Flooding along with additional nitrogen (F.N, F.2N) promoted the plant height of WT as compared to the WC both in monoculture and cocultivation (Figure 2a).

Table 2. Three-way ANOVA on effect of water (W), nitrogen (N), and culture (C) on functional traits of dry weight, specific leaf area, plant height, leaf nitrogen, and chlorophyll content.

Factors	Dry Weight	SLA	Plant Height	Leaf Nitrogen	Chlorophyll Content
W	324.9 **	29.90 **	38.804 **	170.63 **	28.239 **
N	3,486.66 **	44.36 *	118.291 **	6.53 *	110.400 **
C	2,114.12 **	14.09 **	2.02 ^{NS}	4.07 ^{NS}	135.467 **
W ×N	297.23 **	79.53 **	21.33 *	2.56 ^{NS}	2.475 ^{NS}
W × C	4.147^{NS}	3.652^{NS}	5.82 **	43.46 **	3.51 ^{NS}
N × C	665.32 **	8.28 **	7.07 **	45.07 *	4.961 *
W × N × C	324.98 **	3.65 **	8.51 **	34.12 *	11.97 **

* Significant at $p < 0.05$, ** significant at $p < 0.01$. ^{NS} Non-Significant at $p < 0.05$.

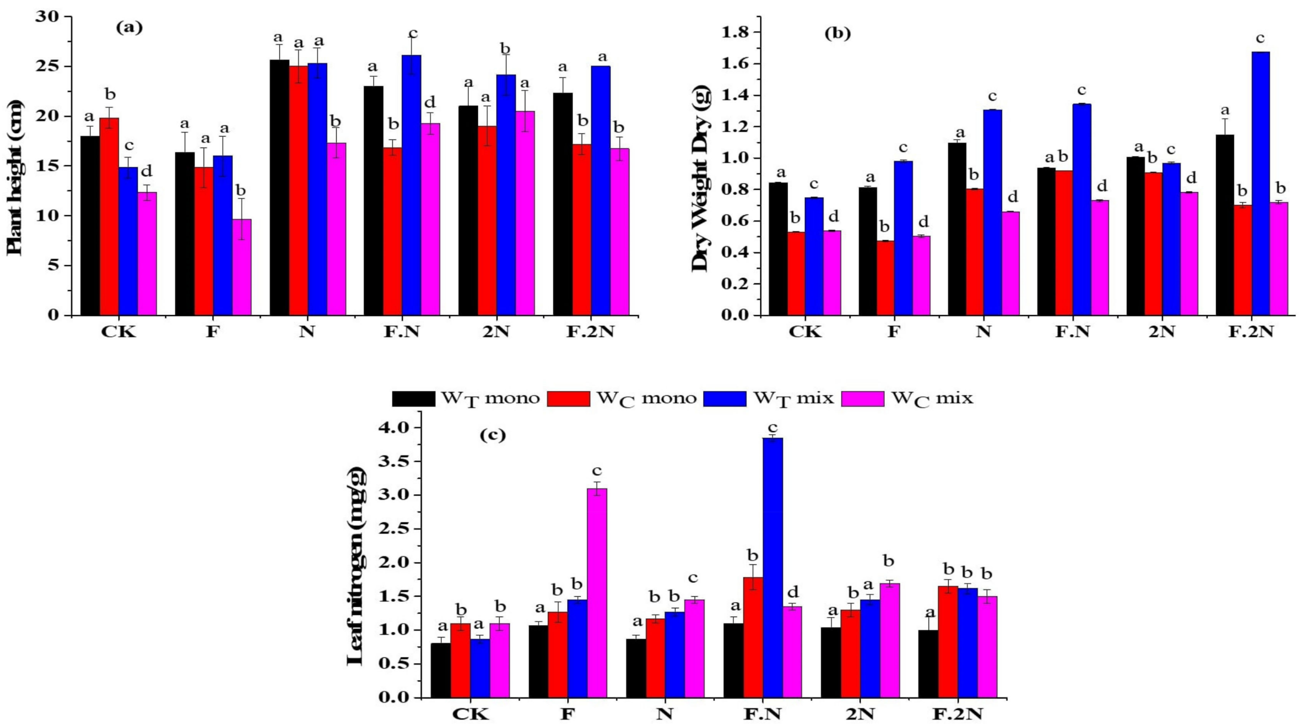

Figure 2. Plant height (**a**), dry weight (**b**), and leaf nitrogen (**c**) of Wedelia trilobata and Wedelia chinensis under different treatments. Mean ± SE and different letter represented significant difference under mono- and cocultivation of Wedelia trilobata and Wedelia chinensis, according to ANOVA and Tukey Test ($p < 0.05$). Note: WT mono = Wedelia trilobata under monoculture, WC mono = Wedelia chinensis under monoculture, WT mix = Wedelia trilobata under mixed culture, WC mix = Wedelia chinensis under mixed culture.

Dry weight (DW) of both the species was significantly affected in all the treatments i.e., W, N, C and their interaction W × N × C (Table 2) with an exception in the case of W × C. DW of WC was low in all the treatments under monoculture and cocultivation compared to the WT. The growth rate of WC was much lower than WT under the control treatment (CK) (Figure 2b). WT had significantly higher growth in all treatments, but higher DW was found in flooding along with additional nitrogen treatments (F.N and F.2N) under cocultivation. These higher DW values indicated that aboveground and belowground biomass of WT was increased a under nutrient-rich environment and outcompeted the competitor (Figure 2b).

Leaf nitrogen (LN) of both the species varied significantly in all the treatments, i.e., W, N, and their interaction W × N × C (Table 2). In the cocultivation at CK, F, and N treatments, LN of WC was higher than WT. While under flooding and additional nitrogen treatments (F.N and F.2N), leaf nitrogen was higher in WT than in WC, indicating that nitrogen addition and water make WT more dominant than WC. In the single factor analysis like flooding (F) and nitrogen (N, 2N), WC had significantly higher leaf nitrogen than WT. While in the combination of nitrogen and flooding (F.N and F.2N), WT was more successful than WC (Figure 2c).

SLA of both the species was significantly affected by all treatment factors, i.e., W, N, C and their interaction W × N × C (Table 2). WT had a higher SLA than WC in all the treatments due to WT's higher leaf area and DW. The SLA of WT was much higher under cocultivation in flooding and additional nitrogen treatments (F.N and F.2N). This indicated that resource richness makes invasive species more dominant than native (Figure 3a).

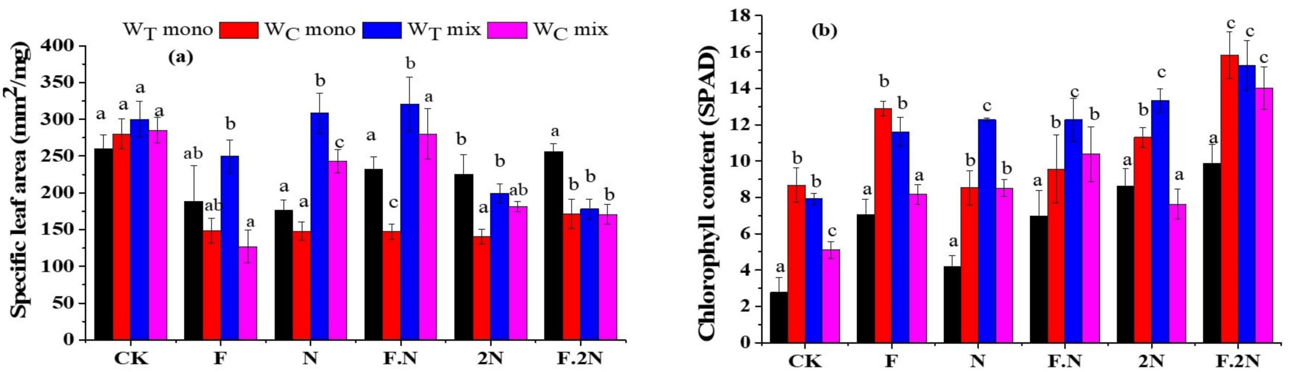

Figure 3. Specific leaf area (**a**) and chlorophyll content (**b**) of Wedelia trilobata and Wedelia chinensis under different treatments; Mean ± SE and different letter represented significant difference under mono and cocultivation of Wedelia trilobata and Wedelia chinensis, according to ANOVA and Tukey Test ($p < 0.05$). Note: WT mono = Wedelia trilobata under monoculture, WC mono = Wedelia chinensis under monoculture, WT mix = Wedelia trilobata under mixed culture, WC mix = Wedelia chinensis under mixed culture.

Chlorophyll contents (CHI) were significant in all treatments, i.e., W, N, C, and their interactions W × N × C, except W × N (Table 2). In monoculture under all treatments, chlorophyll content of WT was lower than WC. While in cocultivation, WT had higher chlorophyll content than WC (Figure 3b). Chlorophyll contents of both the species under flooding and additional nitrogen treatments (F.N and F.2N) were higher than CK, indicating high nitrogen and water made both the species more successful under natural conditions.

3.2. Phenotypic Plasticity Index

F, N, C, and their interaction (W × N × C) significantly affected the phenotypic plasticity index of both species (Table 3). Dry weight and LN were nonsignificant under W × C, and W × N; while F, N, C, and their interactions, i.e., W × N, W × C, C × N and W × N × C, had a significant effect on the phenotypic plasticity index of plant height, DW, SLA, chlorophyll content and leaf nitrogen (Table 3). Out of the five traits, SLA was the most plastic (F = 118.712, $p < 0.01$), with a range of 0.13 to 0.325 (Figure 3b). The plasticity index was higher in all traits of WT as compared to WC, except LN and CHl ($p < 0.05$, Figure 4a).

Table 3. Three-way ANOVA on effect of W, N, and C on plasticity indices of specific leaf area, plant height, dry weight, chlorophyll content, and leaf nitrogen.

Factors	SLA	Plant Height	Dry Weight	Chlorophyll Content	Leaf Nitrogen
W	67.19 **	147.58 **	42.49 **	239.56 **	228.25 **
N	273.83 **	201.69 **	16.98 **	174.04 **	147.42 **
C	95.25 **	53.88 **	44.51 **	1,130.26 **	110.61 ^{NS}
W ×N	43.84 **	192.82 **	64.32 **	322.92 **	100.19 **
W × C	2.47 ^{NS}	16.76 *	5.43 *	29.16 **	244.38 *
N× C	36.784 **	33.71 **	16.42 **	73.07 **	3.02 ^{NS}
W× N × C	118.712 **	21.94 *	10.43 **	69.04 **	123.18 **

* Significant at $p < 0.05$, ** significant at $p < 0.01$. ^{NS} Non-Significant at $p < 0.05$.

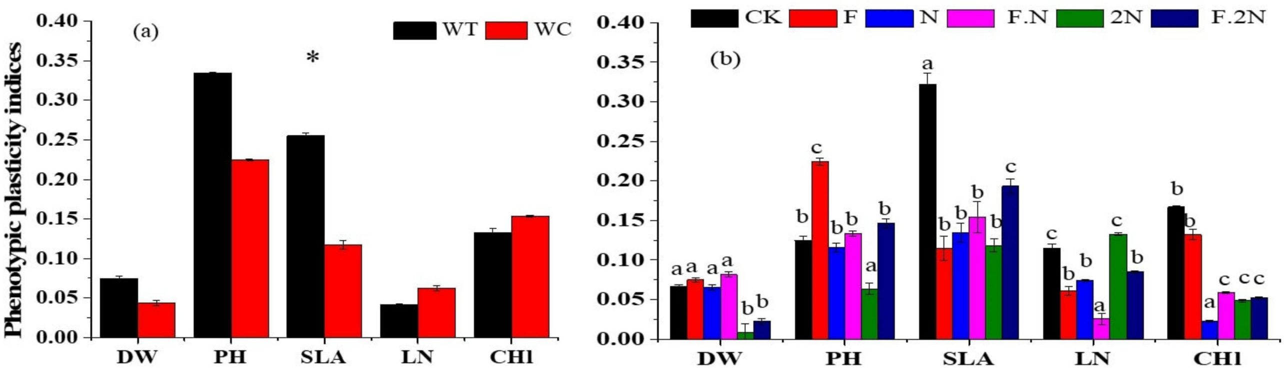

Figure 4. Difference in phenotypic plasticity indices of functional traits of Wedelia trilobata and Wedelia chinensis between plant species and different treatments under cocultivation. (**a**) representing functional traits between both species and (**b**) representing functional traits under different treatments. Mean ± SE and different letters indicate a significant difference ($p < 0.05$) measured by ANOVA among groups followed by Tukey Test. Note: WT = Wedelia trilobata, WC = Wedelia chinensis. * Significant at $p < 0.05$.

3.3. Relative Competition Intensity (RCI)

The relative competition intensity (RCI) gave us variable results for traits of both the species, some of which were positive and others were negative (Figure 5). Plant height, dry weight, SLA, LN, and CHl of WT combined with additional nitrogen and flooding (F.N, F.2N) were affected negatively and showed strong competition. Moreover, plant height of WC in most treatments had RCI below zero, showing strong competition, and SLA, dry weight, and CHl, under the interaction of nitrogen and flooding (F.N and F.2N), were positive (Figure 5). WT became a competitor, and WC became a facilitator, especially under additional nitrogen and flooding (F.N, F.2N).

3.4. Correlations of Competition with the Plasticity of Plant Traits

Competition with the plasticity of plant traits was checked for each species under each treatment and their combinations within monoculture, giving us variable results with the help of Pearson Correlations. F and N reduced the root weight ratio (RWR) of WT (33.91%, −37.73%) and WC (−83.4%, −90.1%) showed a negative correlation. F increased shoot weight ratio (SWR), the relative growth rate of dry weight (RGR_B) and the relative growth rate of shoot length (RGR_{Sl}) of WT (33.9%, 87.2% and 94.2%) and WC (83.4%, 29.6%, and 10%) these showed a positive correlation. N reduced the RGR_B, $RGR_{Sl,}$ and RWR of WC (−59.9%, −18.1%, −90.2%) showed a negative correlation. RGR_B, and RGR_{Sl} increased WT (79.3%, 94.5%) with positive a correlation under N. The combination of flooding and additional nitrogen (F.N, F.2N) decreased the RGR_B of WC (−94.25%, −92.0%) with a negative correlation, but increased the RGR_B of WT (42.0%, 33.9%) compared to CK.

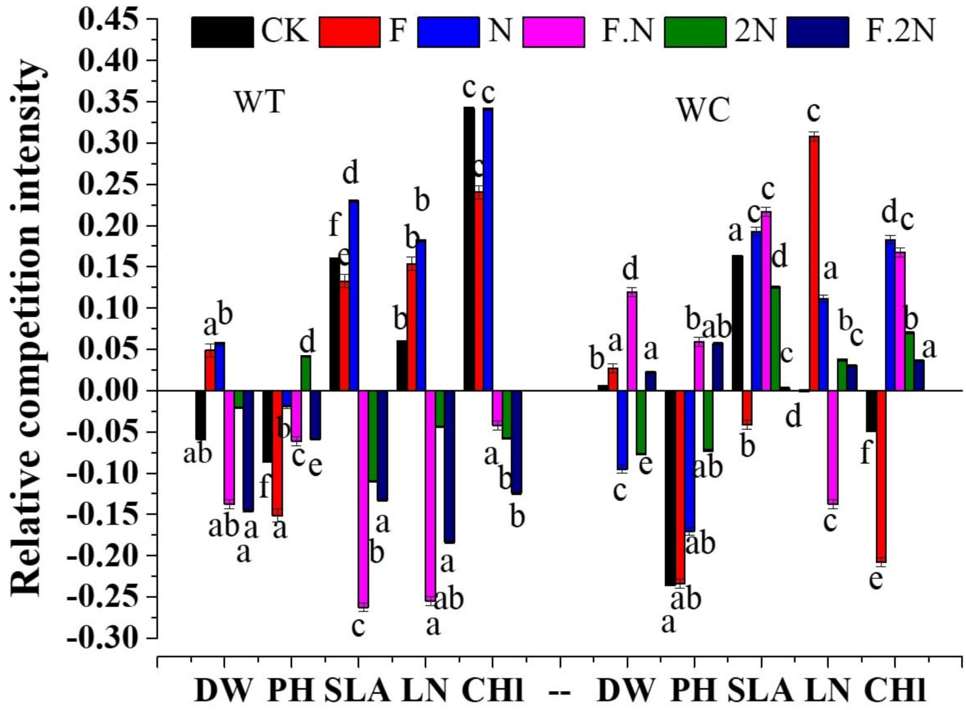

Figure 5. Relative competition intensity of dry weight, plant height, specific leaf area, leaf nitrogen, and chlorophyll content of Wedelia trilobata and Wedelia chinensis under different nitrogen and water treatments in Cocultivation; Mean ± SE and different letters indicate a significant difference; according to ANOVA among groups followed by Tukey Test ($p < 0.05$). Note: WT = Wedelia trilobata, WC = Wedelia chinensis.

4. Discussion

4.1. Functional Traits under Treatments

Water and nitrogen are two main environmental factors that enhance the growth and spreading of plants [30]. Therefore, the invasion process of invasive plant species is mostly dependent upon the availability of water resources and nitrogen amount in the water or soil [31]. This study confirmed that flooding and additional nitrogen promoted the growth of invasive plant species because of higher plant height, dry weight, and SLA. Flooding with higher nitrogen concentration added more biomass in the form of aboveground and belowground biomass. These conditions could enhance the O_2, CO_2, and light uptake that is helpful for WT to promote its growth [12,32]. Several researchers also described that high nitrogen concentrations overcome the stress of flooding and encourage plants to grow, especially invasive plant species [32–34]. WT was notably taller than WC under nitrogen additional and flooding conditions regardless of plant culture (monoculture and cocultivation) (Figure 2a). WC facing oxygen deficiency under flooding in both plant cultures (monoculture and cocultivation), which is why its growth is slower than that of WT [35]. WT plant height was higher than WC in cocultivation due to high phenotypic plasticity and negative effect under the competition (Figure 5). Our results were supported by previous studies that indicated that flooding along with nitrogen promotes the growth of invasive plant species [36]. Therefore, WT and WC can survive in nitrogen enrichment and flooding conditions due to elongation of plant height that was plant approach to survive with these conditions [37,38]. Plant height increment was plant response to flooding and high nitrogen, to get connect with air and sunlight to do photosynthesis process for its growth development [39]. WT may be more competitive in resource acquisition due to its height, particularly for water and nitrogen, which may be the most dominant ecological factor affecting plant growth and survival [36,40]. In addition, the SLA of WT was larger than WC, supposedly due to larger leaf area and traits response under resource-rich habitats [41]. Some studies pointed out a higher growth rate; due to more biomass of leaf rather than leaf structure per unit area [42,43]. At the same time, many plant species enhance their growth rate by increasing leaf area, SLA, and leaf transpiration rate [44]. However, the SLA of WC was significantly lower than WT in all the treatments under both the cultures, except only CK (Figure 3a). This indicated that WC has lower growth rate and not able to utilize resources as compared to that of WT [45]. Hence, SLA may play an important role in the successful invasion of WT. In this study, the higher plant height of WT serves as a strategy to enhance competition for light; however, this imposes a cost in the form of structural support and water transport [46]. Therefore, plant species can have a higher relative growth rate by increasing plant height and decreasing SLA (Figures 2a, 3a and 5), especially in high nitrogen and flooding conditions [40].

Generally, nitrogen and water promote plant growth with increasing DW and RGR_B [35,47]. The same trend was reciprocated in this study (Table 2, Figure 2b). DW of WT was higher under cocultivation because of higher plant height and leaf area [33]. It reduced the effect of oxygen deficiency that was created by flooding conditions [48]. Higher leaf area enhances photosynthesis and transpiration capacity under flooding and nitrogen enrichment conditions [6,26]. Therefore, WT has a higher ability for resource absorption than WC. It also has a higher relative growth rate along with reduced resource investment per unit area under the combination of nitrogen and flooding [49].

4.2. Role of Relative Competitive Intensity and Plasticity Index

Flooding and nitrogen enrichment significantly impact the interspecific competition in the water fluctuation habitat [50]. Relative competition intensity (RCI) is the trade-off among plants between competition and facilitation, which means that under higher resources availability plant shows competition. While under stressful conditions plant exhibits facilitation [51]. RCI of most functional traits under additional nitrogen and flooding (2N and F.2N) were negative of WT. It indicated that WT was more competitive than WC, under cocultivation, because of higher belowground biomass and up to ground biomass under nutrient-rich water conditions [9]. WC might face two factors: competition with WT and sensitivity to flooding with higher nutrients availability [12]. WC has an advantage in competition because of the higher value of phenotypic plasticity (Figure 4) that makes them able to cope with these environmental conditions [45]. This type of outcome mainly happens under these conditions because every plant species has different tolerance under adverse environments [52]. Here, WT appears to be capable of sustaining its growth and alleviating the negative effect of flooding and nitrogen enrichment [39].

Furthermore, RCI under the combination of flooding and additional nitrogen (F.N and F.2N), plant height and SLA of WT had negative values. However, WC had positive values for these parameters, which indicated that WT became a competitor, but W_C behaved like a facilitator [53]. This can be explained by the flaring of the functional divergence between WT and WC under the combination of nitrogen and flooding treatments.

Functional traits observed in this study revealed phenotypic plasticity to some extent (Figure 4). Phenotypic plasticity is the traits mechanism that allows plants to cope with biotic and abiotic environments [51]. It is the main factor for the success of different plants under different habitats [54]. According to the results, it was evident that phenotypic plasticity may play a vital part to adapt the adverse changes in the environments. Phenotypic plasticity and relative competitive intensity are closely related to each other. Both make invasive plant species alter above and below ground functional traits to cope with a wide range of environmental changes [29]. Conflicting to prediction, phenotypic plasticity of LN and CHI in WT were lower than in WC. These lower ranges may indicate a fitness cost for plastic physiological traits under complex environments [2]. Leaf construction costs and plant growth rate may be quiet due to the lower phenotypic plasticity of LN and CHI [40]. WT compensated for the harmful effects of these adverse environments due to the limited plasticity of functional traits [55]. Thus, this facilitates invasion and the development of populations in new habitats [46]. However, the plasticity of other indices of WT was significantly different from WC (Figure 4). Although invasive plant species mostly did not show a higher range of plasticity compared with the natives. In this study, WT showed higher plasticity than WC because of higher resources acquisition. WT and WC also showed higher plasticity in plant growth under the combination of W × N, which enhanced their competitiveness [8,35].

5. Conclusions

Functional traits of WT and WC played an essential role in the successful growth development under nitrogen enrichment and flooding conditions. The dry weight and morphological traits of WT were significantly higher than that of WC under the combination of flooding and additional nitrogen (F.N and F.2N) because of WT's higher resources acquisition ability over WC. LN and CHI of WT were significantly lower than that of WC; this may confer higher resistance to WT under adverse environments. Higher phenotypic plasticity and negative effect of the competition of WT over WC make WT more successful within these complex environments. This study helped us understand the role of functional traits in the successful invasion of invasive plant species.

Author Contributions: Conceptualization, A.A. (Ahmad Azeem) and Q.J.; methodology, A.A. (Ahmad Azeem); software, Q.J.; validation, M.W., A.A. (Ahmad Azeem) and Q.J.; formal analysis, A.A. (Adeel Abbas); investigation, A.A. (Adeel Abbas); resources, M.W.; data curation, Q.J.; writing—original draft preparation, A.A. (Ahmad Azeem); writing—review and editing, T.C.; supervision, T.C.; project administration, M.W.; funding acquisition, T.C. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by Key projects of national key R & D plan and intergovernmental international scientific and technological innovation cooperation (2021YFE0101100).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data of this study will be provided.

Conflicts of Interest: The authors declare no conflict of interest.

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