

Article

Habitat Effect on Allometry of a Xeric Shrub (*Artemisia ordosica* Krasch) in the Mu Us Desert of Northern China

Weiwei She ¹, Yuqing Zhang ^{1,2,*}, Shugao Qin ^{1,2}, Bin Wu ^{1,2}, Zhen Liu ¹, Jun Liu ¹ and Wenjin Zhang ¹

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¹ Yanchi Research Station, School of Soil and Water Conservation, Beijing Forestry University, Beijing 100083, China; wwshe@bjfu.edu.cn (W.S.); qinshugao204@163.com (S.Q.); wubin@bjfu.edu.cn (B.W.); shuibaoliuzhen@bjfu.edu.cn (Z.L.); liujunliuyu@126.com (J.L.); 459318207@qq.com (W.Z.)

² Key Laboratory of Soil and Water Conservation and Desertification Combating of the Ministry of Education, Beijing Forestry University, Beijing 100083, China

* Correspondence: zhangyqbifu@gmail.com; Tel.: +86-10-6233-6172; Fax: +86-10-6233-8689

Abstract: Allometric models are useful for assessment of aboveground net primary productivity (ANPP) and aboveground biomass (AGB) of forests and shrubs, and are widely implemented in forest inventory and management. Multiple forms of allometric models have been used to estimate vegetation carbon storage for desert shrubland, but their validity for biomass estimation has not been tested at a region scale with different habitats. To verify the validity of habitat-specific models, general models (combining data from all habitats/sites), and previously developed models for biomass prediction, we developed both general models and habitat-specific models for aboveground biomass and ANPP of *Artemisia ordosica* Krasch, a dominant shrub of the Mu Us Desert. Our results showed that models based on crown area or canopy volume consistently explained large parts of the variations in aboveground biomass and ANPP. Model fitting highlighted that general allometric models were inadequate across different habitats, and habitat-specific models were useful for that specific habitat. Previous models might be inappropriate for other sites because of site quality differences. There was a strong habitat effect on the allometric relationships of *A. ordosica*. Although our study is a case in point, the results indicate that allometric models for desert shrubs should be used with caution and require robust validation if adopted from other studies or applied to different sites/habitats.

Keywords: allometry; *Artemisia ordosica*; biomass; desert shrubland; net primary productivity

1. Introduction

Allometric models are useful for assessment of aboveground-biomass (AGB) and net primary productivity (ANPP) of forests [1–3] and shrubs [4–6]. They are widely utilized for forest inventory and management because they offer a non-destructive, relatively accurate, and labor-efficient method [7,8]. The aboveground biomass and ANPP of plants are important components of the global carbon cycle. Aboveground biomass can be used in quantifying carbon stores in plants, by using plant carbon density; and ANPP can help to understand potential future carbon storage. Thus, the prediction of aboveground biomass and ANPP of plants will help to evaluate terrestrial carbon sequestration, which is important for mitigation of global climate change [9,10].

Shrubland is one of the major types of terrestrial ecosystems, particularly in drylands, which hold large stores of vegetation carbon [11]. Shrubs accounted for approximate 30% of the

forest carbon sink in the 1980s in China [12], and approximately one-third of the carbon sink in the United States [13]. Drylands occupy about 41% of the Earth's land surface, in which desert shrubland is widely distributed [14,15]. In recent years, scientists and policy-makers have expressed increasing concern regarding carbon sequestration in such areas [16–18]. Allometric models have been widely applied to regional carbon storage estimations for these areas, but their validity for biomass estimation has not yet been tested at a region scale with different habitats [17,19,20]. Specifically, the plausible application of these models took four forms: (i) models developed at a specific site were applied to multiple sites; (ii) models developed in multi-sites were applied to multi-sites; (iii) previously developed models were applied to present conditions; (iv) hybrid forms of the above three schemes. These models are suitable for small areas or study sites, but their validity at large scales might be questioned. In addition, most of these biomass models do not provide raw data and lack proper descriptions of the study site or sampling design. This missing information is a major obstacle for sustainable forestry practices. De-Miguel *et al.* [21] developed a new approach (generalized mixed-effects meta-models) for large-scale biomass prediction, which combined information from published biomass equations and took into account the unknown differences between different locations. This approach may contribute to accurate large-scale biomass predictions, although the application of this method has not been yet widely used in biomass prediction. It is well documented that site/habitat quality has a remarkable influence on intra-specific differences in forest allometric relationships [22–24]. However, it is unclear whether habitat quality has a significant impact on shrub allometric relationships in drylands, which are highly heterogeneous environments with distinct habitats.

The Mu Us Desert is a semi-arid area of 39,800 km², consisting of highly distinctive habitat types (semi-fixed dunes, fixed dunes, and fixed dunes covered with biological soil crusts) [25,26]. *Artemisia ordosica* Krasch is an endemic species that overwhelmingly dominates a wide range of habitats [25]. Although several allometric models for *A. ordosica* have been established previously, most do not evaluate the influence of habitat on allometric equations [27–30]. Natural conditions and previous research conducted in the Mu Us Desert provide an ideal foundation for testing the validity of allometric models for shrubs across differing habitats.

We developed general models and habitat-specific models for aboveground biomass and ANPP of *A. ordosica* in the Mu Us Desert, and also established biomass models for plant components (dead material and woody parts). Our main goals were to (i) test whether habitat-specific models were adequate for different habitats; (ii) evaluate whether general models were adequate for different habitats; and (iii) to assess whether previously developed models were adequate for present conditions.

2. Materials and Methods

2.1. Study Species

A. ordosica is a xeric deciduous multi-stem shrub between 50 and 100 cm in height [25]. Its tap roots can reach 3 m below ground, and lateral roots mainly occur at depths of 0–30 cm [31]. The shoots consist of current-year shoots (purple) and previous-year shoots (brown) with plumose, linearly lobate leaves. The current-year shoots consist of vegetative shoots and reproductive shoots. Vegetative shoots overwinter and bear new vegetative or reproductive shoots the following year, whereas reproductive shoots die during winter [31].

2.2. Research Site

This investigation was conducted at the Yanchi Research Station (37°04'–38°10' N, 106°30'–107°41' E, 1550 m above sea level) situated on the southwestern margin of the Mu Us Desert, Ningxia, China. The climate is mid-temperate, semiarid continental, and monsoonal, with a long-term mean annual temperature of 8.1 °C and an average annual rainfall of 284 mm (1954–2014).

The landscape of the area comprises typical inland dune ecosystems associated with mobile, semi-fixed, and fixed dunes. The soil type is quartisamment, based on U.S. Soil Taxonomy. The vegetation type is a desert shrubland, dominated by *A. ordosica*, with sparse *Hedysarum mongolicum*, *Salix psammophila*, *Caragana korshinskii*, and *Agropyron cristatum*. In well-fixed dunes, the ground surface is largely covered by biological soil crusts. The sampling field is part of an enclosed area, within which vegetation has recovered from grazing prohibition for ten years [32] and this study site is a mature shrubland community.

2.3. Experimental Design and Data Collection

At the end of the growing season (late August, 2014), three plots (15 × 15 m, 15 × 15 m, and 20 × 20 m) were selected in fixed dunes covered with biological soil crusts (FC), fixed dunes (FD), and semi-fixed dunes (SF), respectively, (Figure 1) according to their vegetation coverage [33]. These habitats were located 2–4 km from each other. In all plots, we measured shrub height (H) and crown dimensions (maximum crown width (C_1), and minimum crown width (C_2)). With these variables, shrub crown area (CA) and canopy volume (V) were calculated as $CA = \pi \times C_1/2 \times C_2/2$ and $V = CA \times H$, respectively. Shrub size distribution was estimated from canopy area. 31 individual plants were selected from each plot for the harvest procedure via stratified systematic sampling based on the shrub size (three strata with $CA < 0.5 \text{ m}^2$, $0.5 < CA < 1.0 \text{ m}^2$, $CA > 1.0 \text{ m}^2$). Subsequently, individuals were harvested and then separated in the laboratory into current-year shoots, woody parts, and dead material. All plant samples were oven-dried at 70 °C for 48 h and weighed.

In this study, we took the biomass of current-year shoots as an estimate of shrub annual ANPP, which could be easily identified by direct observation of color and structure [34]. ANPP might be slightly underestimated due to not taking the growth of older branches into consideration, but this estimation method was successfully applied to shrub ANPP evaluation in the Patagonian steppe [34] and Mediterranean rangeland [35].

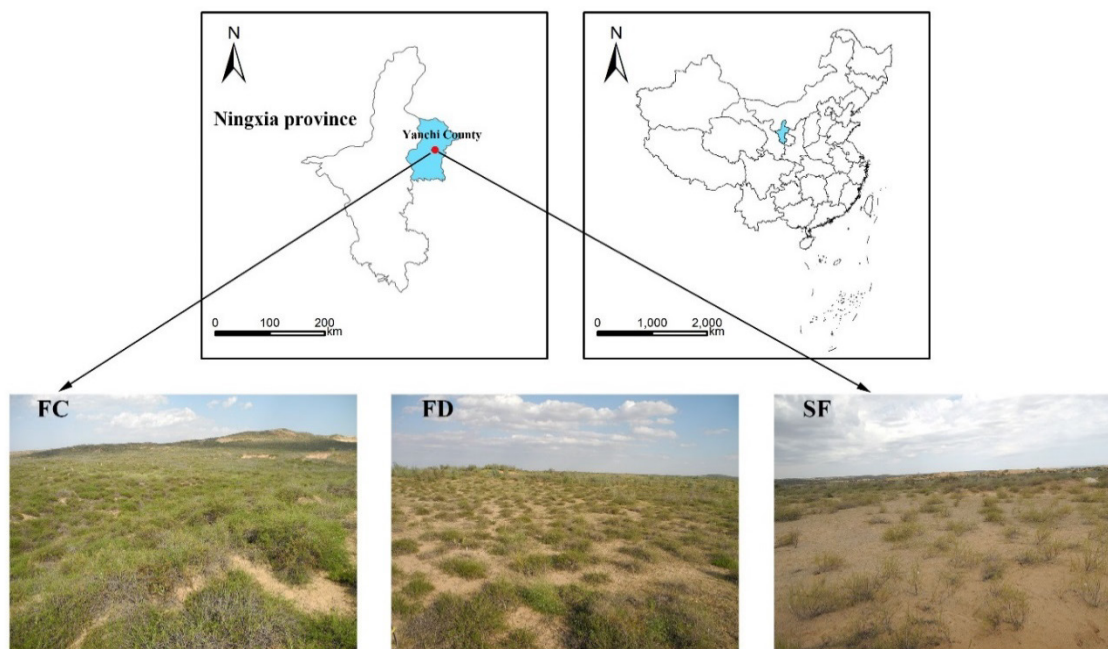


Figure 1. Map of the study site, and pictures of three distinct habitats: FC (fixed dunes covered with biological soil crusts), FD (fixed dunes), and SF (semi-fixed dunes).

Soil samples were collected from 0 cm to 20 cm depth in early September, 2014. Three soil cores were taken from each plot using a 3.8 cm diameter soil auger. All soil samples were air-dried and sieved through 2 mm screens for soil bulk density, pH measurement, and then ground to pass

through a 0.15 mm mesh for analysis of soil total nutrients. Soil bulk density was determined by a volumetric soil sampler (100 cm³). Soil pH was measured in a soil/water (1:2.5) suspension using a pH meter (PHS-3C, Zhiguang Instruments, Shanghai). Soil organic carbon (SOC) was analyzed by the potassium dichromate oxidation method, soil total nitrogen (TN) by the micro-Kjeldahl method, and soil total phosphorus (TP) by the Mo-Sb Anti spectrophotometer method. The vegetation and soil characteristics of each habitat are displayed in Table S1. Table S2 provides a statistical summary of the sample plants (*n*), independent variables (*CA* and *V*), and dependent variables (*Biomass* and *ANPP*) by habitat and *CA*-classes.

2.4. Model Development, Selection, and Evaluation

We focused on establishing general allometric models combining data from all three habitats and habitat-specific models for the prediction of aboveground biomass and ANPP of *A. ordosica*. Biomass models for dead material and woody parts were also tested. All models were developed with *CA* and *V* as independent variables.

We tested three equations for the estimation of shrub biomass and ANPP, which have been commonly applied to shrub species [36–38].

$$\text{Linear : } Y = \beta_0 + \beta_1 X \quad (1)$$

$$\text{Quadratic : } Y = \beta_0 + \beta_1 X + \beta_2 X^2 \quad (2)$$

$$\text{Power : } Y = \beta_0 X^{\beta_1} \quad (3)$$

where *X* is an independent variable, *Y* is a dependent variable, and $\beta_0, \beta_1, \beta_2$ are model parameters.

For the evaluation of models, several parameters (R^2 , *RMSE*, %*bias*, and %*ae*) were established, where: R^2 is the coefficient of determination, *RMSE* is the Root Mean Square Error (g), relative mean prediction error (%*bias*) is used to access model accuracy, absolute mean prediction error (%*ae*) is used to evaluate the precision of the model, and relative error (*RE*) is the percent difference between observed and predicted biomass. These parameters were defined as:

$$RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n (e_i)^2} \quad (4)$$

$$\%bias = \frac{1}{n \times MB} \sum_{i=1}^n e_i \times 100 \quad (5)$$

$$\%ae = \frac{1}{n \times MB} \sum_{i=1}^n |e_i| \times 100 \quad (6)$$

$$RE(\%) = (Biomass_{observed} - Biomass_{predicted}) / Biomass_{observed} \times 100 \quad (7)$$

where e_i is the residuals (difference between observed and predicted biomass) and *MB* is the mean observed value.

The most appropriate prediction model was selected based on the highest value of R^2 and the lowest values of *RMSE* and %*bias*. General models were evaluated across habitats based on the dataset of the specific habitat according to the values of %*bias* and %*ae*. The empirical acceptable value of %*bias* was between −10% and 10% [39]. Some previously developed models were tested on the dataset used in this study in order to assess their potential application, using the following procedures and assumptions:

- (i) For Jin *et al.* [27] (39°29' N, 110°11' E, northeastern Mu Us Desert), we evaluated aboveground biomass (kg) ($Biomass = 0.010 \times (D \times H)^{1.234}$) and ANPP (kg) ($ANPP = 0.053 \times (D \times H)^{0.886}$) with $(D \times H)$ as independent variables. D represents crown diameter, and is the mean value of C_1 and C_2 .
- (ii) For Liu *et al.* [28] (37°30'–39°20' N, 107°20'–111°30' E, eastern Mu Us Desert), we evaluated aboveground biomass (kg) ($Biomass = 0.028 + 1.693V$ and $Biomass = 1.154 \times CA^{1.257}$) with V and CA as independent variables. The models of Liu *et al.* [28] were general models combining data from three habitats (fixed dune, semi-fixed dune and shifting dune).

We also presented uncertainty levels (*UL*) (the standard deviation of %*bias* between the study habitats, see Alvarez *et al.* [39]) of all previous models and selected general models for assessing the uncertainty of these models when applied to different habitats.

Analysis of covariance (ANCOVA) was used to assess whether the allometric relationship differed significantly ($p < 0.05$) between habitats. All data were tested to confirm normality and homogeneity of variances. Student *t*-tests were performed for all habitats to determine whether the %*bias* or %*ae* values were significantly different from zero. All analyses were performed using SPSS statistical software (version 20.0, SPSS Inc., Chicago, IL, USA).

3. Results

Allometric relationships for the prediction of aboveground biomass and ANPP with CA as independent variable are presented in Table S3. For aboveground biomass, the power model presented the lowest *RMSE* values and highest R^2 values for the general model and the habitat-specific model for SF. The quadratic and linear models showed the best performances for FC and FD, respectively. All parameter estimates of these models were significant, thus these models were selected (bold in Table S3). The R^2 for the selected habitat-specific models ranged from 0.86 to 0.93, while that for the general model was 0.70. For ANPP, the quadratic, power, power, and linear models provided the best fit for FC, FD, SF and the general condition, respectively, based on their *RMSE* and R^2 values. Moreover, these selected models had significant parameter estimates. The R^2 for the selected habitat-specific models ranged between 0.76 and 0.83, while that for the general model was 0.63.

Allometric equations of aboveground biomass and ANPP with V as an independent variable are listed in Table S4. For both aboveground biomass and ANPP, only the power model had significant parameter estimates, therefore it was selected. The R^2 values for the habitat-specific models of aboveground biomass and ANPP were within the ranges 0.81–0.91 and 0.64–0.79, respectively. The R^2 values for the general models of aboveground biomass and ANPP were 0.68 and 0.65, respectively.

The best-fit models for the biomass of dead material and woody parts in different habitats were derived similarly to that described for aboveground biomass (see Table S5). The R^2 values for the general models of dead material and woody parts were 0.42 and 0.68, respectively, with CA as an independent variable; and 0.33 and 0.70, respectively, with V as an independent variable.

The parameters %*bias* and %*ae* are useful for assessing the accuracy and precision of allometric models. As can be seen in Table 1, the values of %*bias* and %*ae* generally differ greatly between the general level and the habitat level (*i.e.*, lower precision and accuracy) when applying the general models to evaluate aboveground biomass and ANPP across habitats. For FD, the values of %*bias* were quite low for the aboveground biomass models compared with the other two habitats. For the ANPP models, the %*bias* values for SF were lower than the other two habitats. Figure S1 also shows considerable differences in the relative error (*RE*) between the general level and the habitat level. The *UL* levels of the general models varied from 21.4% to 42.6%. High levels of *UL* indicated that the general models were quite unstable at the habitat scale.

Table 1. Evaluation of selected general models with CA (m²) and V (m³) as independent variables across habitats.

Dependent Variable	Model	Habitat	Observed Mean (g)	%Bias	%Ae
Aboveground biomass (CA) UL = 39.0%	Power	FC (n = 31)	469.2	33.6 ^S	43.1
		FD (n = 31)	318.4	−10.9	27.2
		SF (n = 31)	348.6	−44.1 ^S	52.2
		All (n = 93)	378.7	−2.7	41.4
ANPP (CA) UL = 23.4%	Linear	FC (n = 31)	83.0	23.9 ^S	40.1
		FD (n = 31)	66.0	−22.5 ^S	42.1
		SF (n = 31)	108.9	−4.5	49.7
		All (n = 93)	86.0	0.0	44.7
Aboveground biomass (V) UL = 42.6%	Power	FC (n = 31)	469.2	42.2 ^S	44.5
		FD (n = 31)	318.4	−3.8	28.3
		SF (n = 31)	348.6	−43.1 ^S	49.4
		All (n = 93)	378.7	3.1	41.5
ANPP (V) UL = 21.4%	Power	FC (n = 31)	83.0	25.2 ^S	30.9
		FD (n = 31)	66.0	−16.9	43.5
		SF (n = 31)	108.9	−2.4	49.6
		All (n = 93)	86.0	2.8	42.0

^S %bias was significantly different from zero ($p < 0.05$); all %ae values were significantly different from zero ($p < 0.05$).

The same dataset was also used to calculate the %bias and %ae values for some previously developed models (Table 2). For aboveground biomass, the %bias values varied from −270.7 to −58.9% (overestimation) for the models developed by Liu *et al.* [28], and from 97.7 to 99.0% (underestimation) for the models of Jin *et al.* [27]. For ANPP, the %bias values obtained from the model developed by Jin *et al.* [27] ranged between 47.3% and 64.7% (underestimation). All of the previously developed models had high %ae values. Figure S2 also shows that the previous models had large bias with respect to biomass prediction at the habitat scale. The UL for the models of Liu *et al.* [28] varied from 101.3% to 106.7%, while the models of Jin *et al.* [27] varied from 0.7% to 8.9%.

Allometric relationships between aboveground biomass and CA or V, and between ANPP and CA or V were positive, and varied in strength according to habitat (Figure 2). For aboveground biomass, ANCOVA showed significant interactive effects between habitat and CA ($p < 0.01$, $R^2 = 0.82$) (Figure 2A), and between habitat and V ($p < 0.01$, $R^2 = 0.87$) (Figure 2B). Analysis of habitat effect on ANPP showed significant interactive effects between habitat and CA ($p < 0.01$, $R^2 = 0.69$) (Figure 2C), and between habitat and V ($p = 0.01$, $R^2 = 0.70$) (Figure 2D).

Table 2. Evaluation of previously developed models across study habitats.

Model	Dependent Variable	Independent Variable	Habitat	n	Observed Mean (g)	%Bias	%Ae
Liu <i>et al.</i> [28] UL = 101.3%	Aboveground biomass	CA	FC	31	469.2	−70.0	70.4
			FD	31	318.4	−194.1	194.1
			SF	31	348.6	−270.7	270.7
			All	93	378.7	−166.3	166.5
UL = 106.7%		V	FC	31	469.2	−58.9	66.3
			FD	31	318.4	−190.1	190.1
			SF	31	348.6	−270.3	270.3
			All	93	378.7	−160.5	163.6
Jin <i>et al.</i> [27] UL = 0.7%	Aboveground biomass	D*H	FC	31	469.2	99.0	99.0
			FD	31	318.4	98.1	98.1
			SF	31	348.6	97.7	97.7
			All	93	378.7	98.3	98.3
UL = 8.9%	ANPP		FC	31	83.0	64.7	67.0
			FD	31	66.0	47.3	51.7
			SF	31	108.9	59.5	65.8
			All	93	85.95	58.0	62.6

All %bias and %ae values were significantly different from zero ($p < 0.05$).

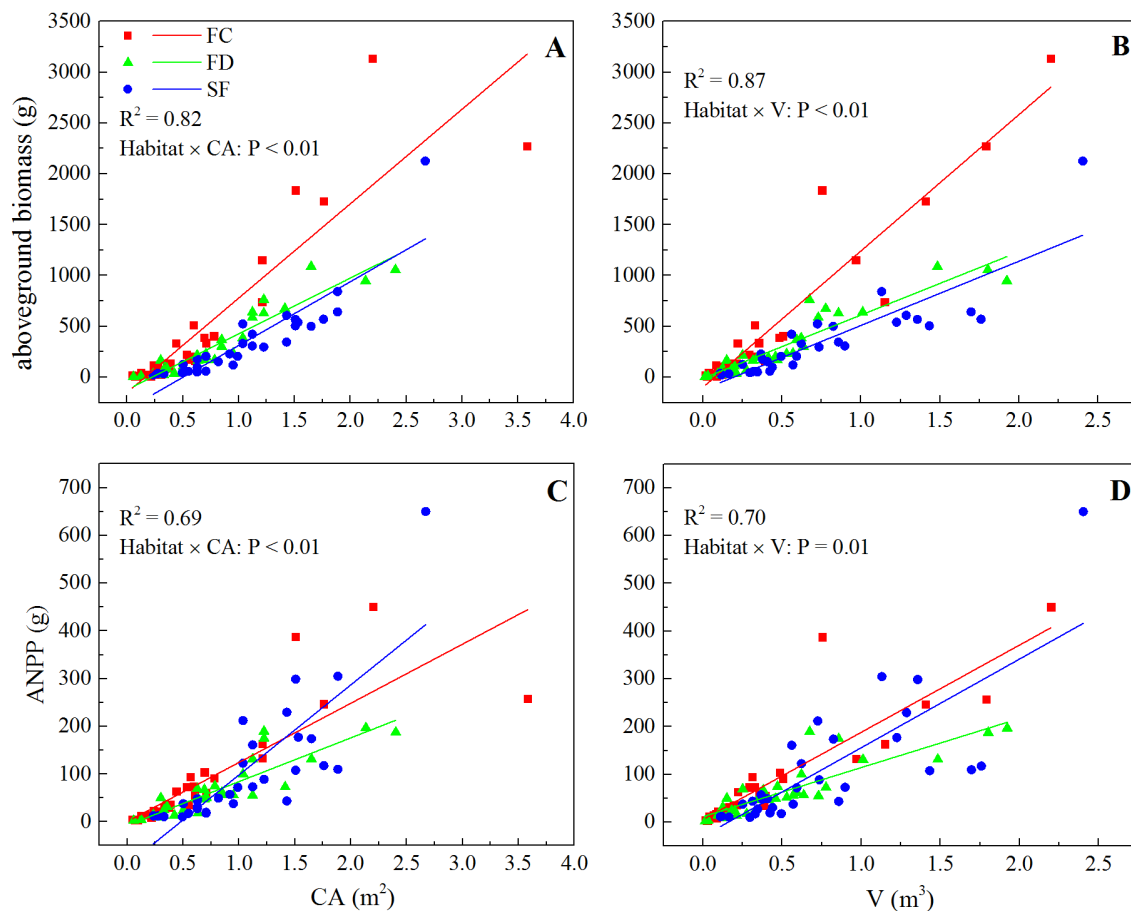


Figure 2. ANCOVA of aboveground biomass *versus* CA (A) and V (B) by habitat, and for ANPP *versus* CA (C) and V (D) by habitat.

4. Discussion

Our study established general models and habitat-specific models for the estimation of aboveground biomass and ANPP of *A. ordosica* based on CA or V, and tested the influence of habitat quality on plant allometric relationships. The best-fit models are shown in bold in Table S3 and S4. There is a strong habitat effect on plant allometric relationships, such that the general models do not fit well across different habitats. Furthermore, the previous models produce large biases when applied to this study.

Allometric equations with CA or V consistently provide good fits for biomass estimates (Table S3 and S4). CA and V can be easily obtained and are commonly applied to biomass prediction for multi-stem shrubs [38], and can be used in different scenarios. CA is appropriate for sand burial conditions, under which *H* is difficult to measure.

In our study, the high levels of *UL* and *%bias* indicate that the general models are inadequate when applied to different habitats (Table 1; Figure S1). Moreover, ANCOVA indicates that the allometric relationships differ significantly between the three habitats (Figure 2). Since the climate is almost the same for the three habitats, the differing allometric relationships are most probably driven by differences in habitat quality (Table S1). Numerous studies have reported that soil water and nutrient availability differ significantly between dune habitats [30,40]. Soil water and nutrient availability, as key drivers of plant growth, could change the allocation of biomass, thus altering allometric relationships [41,42]. Our results highlight that biomass estimation for desert shrubland is reasonably accurate when based on habitat-specific models. However, our study did not fit a

generalized model, which took into account the habitat-specific random effects, because this would have yielded similar results [43].

The previous models developed by Liu *et al.* [28] and Jin *et al.* [27] do not fit our data well (Table 2; Figure S2). Those of Liu *et al.* [28] significantly overestimated aboveground biomass, whereas those of Jin *et al.* [27] significantly underestimated aboveground biomass and ANPP. The plant size range in this study ($CA\ 0.05\text{--}3.58\text{ m}^2$, $V\ 0.01\text{--}2.40\text{ m}^3$) is almost a subset of the data range ($CA\ 0.16\text{--}3.30\text{ m}^2$, $V\ 0.06\text{--}3.63\text{ m}^3$) reported by Liu *et al.* [28], while Jin *et al.* [27] did not provide model data ranges. The missing information related to the model data ranges for the models of Jin *et al.* [27] may contribute to the uncertainty of the model assessment. The high levels of UL for the models of Liu *et al.* [28] indicated that these models were quite unstable at the habitat scale (Table 2). The UL for the models of Jin *et al.* [27] were quite low, which suggested that these models had systematic errors at the habitat scale (Table 2). These results may relate to qualitative differences between sites. The results are as expected, given the differences in allometric relationships between habitats at the same site. Our results suggest that *A. ordosica* is a highly plastic and adaptive species, which alters its ecological adaptive strategies by adjusting biomass allocation in response to differences in site quality. Thus, it is important to note that models developed at a specific site have a limited domain of application. However, it is a common problem that many published models lack basic descriptions of the study location, sampling design, or the statistics associated with the equation [44,45]. This missing information limits the use of allometric models in a transparent and comparable way [45]. Thus, it is important to follow standard guidelines for publishing allometric models [45].

The main aim of developing allometric models is for application to future scenarios. However, allometric relationships for a given species may vary with habitat quality and climate condition [23,24]. Therefore, these relationships may be invalid when environmental conditions appear to change. Global environmental change is a comparatively slow process and will thus have limited effects on drylands within the next few years, whereas interannual climatic variability (e.g., precipitation) could be the key factors linked to plant growth [14]. Since shrub biomass accumulates over the course of several years, it shows a weak response to conditions of the present year (*i.e.*, dry, normal, or wet) [23,46]. However, both a long-term (14 years) observational study [47] and a short-term (three years) rainfall manipulative experiment [48] also indicated that shrub ANPP showed low interannual variation and was only weakly dependent on annual precipitation. Poor response of shrub growth to precipitation could occur largely because the deep roots of these plants are able to utilize water from deep soil layers [49,50]. In addition, the soil water content (SWC) at depth shows a weak response to the pattern of rainfall in the study area [51]. Thus, to the best of our knowledge, our allometric models are more likely to be valid for *A. ordosica* biomass and ANPP prediction in our study area in the next few years. In practice, forest management strategies also recommend that allometric models for particular species should be renewed periodically (20 years for trees) [52]. Moreover, studies on the impacts of habitat-related factors (e.g., topography, soil texture) and climate change-related factors (e.g., temperature increases, changing precipitation patterns) on plant allometric relationships would be one possible direction for further research.

Shrubland is an important ecosystem type in China and accounts for large stores of vegetation carbon [11,12]. However, forest inventories only present the area of shrubland [53], thereby hindering the estimation of carbon sequestration. Our models will help to provide a foundation for the precise assessment of vegetation carbon storage in desert shrubland. Although our models for the prediction of biomass are likely to be highly habitat- and species-specific, our approach could assist scientists and forest managers in developing models in desert shrubland that have distinct habitats. Furthermore, the finding that habitat quality differences strongly influence plant allometric relationships indicates that habitat factors should be considered when evaluating ecosystem biomass or productivity in desert shrubland.

Supplementary Materials: Supplementary materials can be accessed at: <http://www.mdpi.com/1999-4907/6/12/4385/s1>.

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