

Manuscript Number: ECOLIND-7907R3

Title: Estimating aboveground biomass seasonal dynamics of a riparian pioneer plant community: an exploratory analysis by canopy structural data

Article Type: Research paper

Keywords: Three Gorges Reservoir, non-destructive method, Cynodon dactylon, gap fraction, seasonal change, general model

Corresponding Author: Professor Shengjun Wu,

Corresponding Author's Institution: Chongqing Institute of Green and Intelligent Technology, Chinese Academy of Sciences

First Author: Zhaofei Wen, Ph.D.

Order of Authors: Zhaofei Wen, Ph.D.; Maohua Ma, Ph.D.; Ce Zhang, Ph.D.; Xuemei Yi; Jilong Chen; Shengjun Wu, Ph.D.

Abstract: The aboveground biomass (AGB) of vegetation is of central importance in providing ecosystem productivity. Models have already been developed to estimate AGB via canopy structural variables in both fundamental and applied ecological studies. However, the capabilities of canopy structural variables in indicating AGB dynamics throughout the growing season are still unclear. This study focuses on the AGB of the dominant pioneer species *Cynodon dactylon* (L.) Pers. (Bermuda grass) during early succession in newly formed riparian habitat of China's Three Gorges Reservoir (TGR). The aims are (1) to find the most important factor that impacts on AGB in different season, and (2) to develop a best model that can estimate the AGB throughout the growing season with multiple structural variables. We conducted six times of valid field sampling on the *C. dactylon* communities (from May to September in 2016) to develop AGB models. The models were developed based on the following five candidate canopy structural variables: canopy height (H), canopy cover (CC), leaf area index (LAI), the volume related variables VLAI ($H \times LAI$) and VCC ($H \times CC$), and one seasonal growth effect variable (SV). We conducted univariate linear regression analysis to reveal the most important estimator of AGB and the best subsets regression analysis to identify the best models for the estimation of AGB. Canopy structural characteristics of stand are key factors to determine the change of the most important estimators throughout the growth season. Cover was found to be the most important predictor during the early growing season, and VLAI was the most important one for mid and end of the growing season. The developed best models can explain an additional 11% in AGB variance on average throughout seasonal change and compared with those developed with the selected most important estimators. SV was found to be useful to develop a general model to estimate the seasonal AGB throughout the entire growing season. Since the studied structural variables could be obtained over large extent, it is recommended that the models for different growing stages are extend to regional scale. Such an extending application will be useful to provide both empirical and theoretical

explanations for riparian ecosystem functions against water level fluctuated disturbance.

Response to Reviewers: In case of any character and Table that cannot be shown properly in here, the response letter was uploaded as an attachment file.

Dear Dr. Petina Lesley Pert,
Associate Editor
Ecological Indicators

On behalf of my co-authors, we thank you very much for giving us the opportunity to revise the manuscript, and we appreciate the reviewer #3 very much for his/her kind comments and suggestions on our manuscript entitled “Estimating aboveground biomass seasonal dynamics of a riparian pioneer plant species: an exploratory analysis by canopy structural data” (Ms. Ref. No. ECOLIND-7907R2).

We have revised the manuscript according to the reviewer's comments. The revised parts were marked in **red**. In our point-by-point response letter attached below, the reviewer's comments were marked **dark blue**. We guess the reviewer's most concern is that the places of our sampling sites may have impacts on the modeling we conducted and should be verified first. In other words, some of the collected sampling quadrats may not be independent. In the response letter, we tested his/her concern and found that the all the sampling quadrats were independent and the places of the sampling sites have no significant impacts on the modeling. Attached please find the revised version, which we would like to submit for your kind consideration.

Looking forward to hearing from you.

Best regards,

Shengjun Wu
wsj@cigit.ac.cn

Research Center for Ecology and Environment in the Three Gorges Reservoir; Chongqing Institute of Green and Intelligent Technology, Chinese Academy of Sciences

Responses to the Reviewer #3

1
2
3 Reviewer #3: The authors have improved the manuscript. However, the expression of study aims
4 haven't been changed, and the statistic methods should be improved by adding place as a random
5 factor to exclude the impact of place.
6
7

8 **Response:** Thanks. We have responded your comments point-by-point. Details are given below.
9

10
11 1. You have well explained your aims in the response letter, but you didn't change the expression
12 in the manuscript. For my understanding, you used the univariate linear regression model to find
13 the most important factor that impacts on AGB, while use multiple regression model to estimate
14 AGB. Therefore, it is better to say "The aims are (1) to find the most important factor that impacts
15 on AGB in different season, and (2) to develop a best model that can estimate the AGB throughout
16 the growing season with multiple structural variables. Please correct it in the rest part of your
17 manuscript.
18
19
20
21

22 **Response:** Thanks for your kindly suggestion. The relevant text in the manuscript have been
23 revised in the light of your suggestion.
24
25

26 2. Since you collected samples from three places, you should use mixed-effects regression model,
27 and include place as a random effect to check whether place has impact on results. If there is no
28 difference between mixed effects regression results and regression results without random effect,
29 you can use your present model.
30
31
32

33 **Response:** Thanks for your suggestion. We've tried to figure out how to respond this comment.
34 However, we are afraid of not fully understanding the comment. The main confusion is on the
35 term "three places". (1) Do you mean the "place" is "sampling quadrat"? If so, we collected
36 samples not from three quadrats but more than 14 quadrats in a sampling date (Table 1). Moreover,
37 we think the effects of sampling location have been considered. Because those effects can be
38 represented by the different growth time and could be captured by the seasonal growth-effects
39 variable (i.e., SV, L222-228) which has been involved in the modeling processing; (2) do you
40 mean the "three places" are "three gorges"? If so, we are sorry for the confusion because the three
41 gorges is a place name, not three different "places"; (3) or do you mean the "places" are sampling
42 sites? If so, we collected samples from five sites (from A to E) as shown in Fig. 1. Follow your
43 suggestion, for each sampling date, we considered the place (i.e., sites) as a random effect and
44 developed a new linear mixed effects model by lme4 package in R, based on the selected variables
45 in Table 2 and Table 3, respectively. We also developed a corresponding model without
46 considering place as random effect. The difference between the two models was then tested by
47 ANOVA analysis. The results are given here (Table R1). From Table R1, we can generally draw a
48 conclusion that the selected sites did not have significant effects on the models we presented in the
49 study. We added this information in the text, "The places of those sites have been tested (the
50 results were not shown) having no significant effect on the modeling we conducted in the Section
51 2.3." (L183-185). Anyway, we would like very much to discuss with the reviewer, which can
52 definitely help us in improving the manuscript. Thanks!
53
54
55
56
57
58
59
60
61
62
63
64
65

Table R1. Statistical test results of the difference between two linear models with and without considering place as random effect in model.

Sampling dates	Based on the selected variable in Table 2		Based on the selected variables in Table 3	
	Chi-Square value	<i>p</i> -value	Chi-Square value	<i>p</i> -value
May 30-31	0	1	0	1
Jun. 12-13	0.7371	0.3906	6.5239	0.01064
Jun. 21-22	0	1	0	1
Jul. 1-2	1.3209	0.2504	0.5946	0.4407
Jul. 10-11	0	1	0.0494	0.8241
Sep. 22-23	3.7916	0.05151	0.1526	0.6961

3. I also concern whether *Cynodon dactylon* community is mono-species community or multiple-species community. Please state this in the site description. For my understanding it is a mono-species community, but it is better to use "a riparian pioneer plant community" in the title. If it is not pure community, there is impact of other species on biomass as you listed in the introduction line 123-124.

Response: You are right. According to our field survey, the *Cynodon dactylon* community is mono community (see Appendices Fig. A.2) distributing at lowland of elevations roughly below 165 m. We have stated this in L175-176 “In the lowland area, the *C. dactylon* communities are almost mono-species communities which were targeted in the study.” The title also revised according to your suggestion “Estimating aboveground biomass seasonal dynamics of a riparian pioneer plant community: an exploratory analysis by canopy structural data”.

- Seasonal AGB of *C. dactylon* communities in riparian zone of the TGR were estimated
- Variations of canopy structural variables in estimating seasonal AGB were explored
- Canopy cover was detected as the best estimator of AGB in early growing season
- LAI-derived volume variable was found as the best indicator in late growing season
- Seasonal growth effect was useful for estimating AGB for the entire growing season

1 **Estimating aboveground biomass seasonal dynamics of a riparian pioneer plant**
2 **community: an exploratory analysis by canopy structural data**

3

4 Zhaofei Wen^{a, b}, Maohua Ma^a, Ce Zhang^c, Xuemei Yi^a, Jilong Chen^a, Shengjun Wu^{a, *}

5

6 ^a Ecological Process and Reconstruction Research Center of the Three Gorges Ecological
7 Environment, Chongqing Institute of Green and Intelligent Technology, Chinese Academy of
8 Sciences, No. 266, Fangzheng Avenue, Shuitu Hi-tech Industrial Park, Shuitu Town, Beibei
9 District, Chongqing 400714, China

10 ^b University of Chinese Academy of Sciences, No. 19A Yuquan Road, Beijing 100049, China

11 ^c Lancaster Environment Centre, Lancaster University, Lancaster, United Kingdom, LA1 4YQ

12

13 E-mail addresses: wenzhaofei@cigit.ac.cn (Z.F. Wen), mamaohua@cigit.ac.cn (M.H. Ma),
14 c.zhang9@lancaster.ac.uk (C. Zhang), yixuemei@cigit.ac.cn (X.M. Yi), chenjilong@cigit.ac.cn
15 (J.L. Chen), and wsj@cigit.ac.cn (S.J. Wu)

16

17 * Corresponding author.

18 E-mail address: wsj@cigit.ac.cn

19 Postal address: Ecological Process and Reconstruction Research Center of the Three Gorges
20 Ecological Environment, Chongqing Institute of Green and Intelligent Technology, Chinese
21 Academy of Sciences, No. 266, Fangzheng Avenue, Shuitu Hi-tech Industrial Park, Shuitu Town,
22 Beibei District, Chongqing 400714, China.

23

24

25

26

27

28

29

30

31

32

33

34

35

36

37

38

39

40 **Abstract:** The aboveground biomass (AGB) of vegetation is of central importance in providing
41 ecosystem productivity. Models have already been developed to estimate AGB via canopy
42 structural variables in both fundamental and applied ecological studies. However, the capabilities
43 of canopy structural variables in indicating AGB dynamics throughout the growing season are still
44 unclear. This study focuses on the AGB of the dominant pioneer species *Cynodon dactylon* (L.)
45 Pers. (Bermuda grass) during early succession in newly formed riparian habitat of China's Three
46 Gorges Reservoir (TGR). The aims are (1) to find the most important factor that impacts on AGB
47 in different season, and (2) to develop a best model that can estimate the AGB throughout the
48 growing season with multiple structural variables. We conducted six times of valid field sampling
49 on the *C. dactylon* communities (from May to September in 2016) to develop AGB models. The
50 models were developed based on the following five candidate canopy structural variables: canopy
51 height (H), canopy cover (CC), leaf area index (LAI), the volume related variables V_{LAI} ($H \times LAI$)
52 and V_{CC} ($H \times CC$), and one seasonal growth effect variable (SV). We conducted univariate linear
53 regression analysis to reveal the most important estimator of AGB and the best subsets regression
54 analysis to identify the best models for the estimation of AGB. Canopy structural characteristics of
55 stand are key factors to determine the change of the most important estimators throughout the
56 growth season. Cover was found to be the most important predictor during the early growing
57 season, and V_{LAI} was the most important one for mid and end of the growing season. The
58 developed best models can explain an additional 11% in AGB variance on average throughout
59 seasonal change and compared with those developed with the selected most important estimators.
60 SV was found to be useful to develop a general model to estimate the seasonal AGB throughout
61 the entire growing season. Since the studied structural variables could be obtained over large
62 extent, it is recommended that the models for different growing stages are extend to regional scale.
63 Such an extending application will be useful to provide both empirical and theoretical explanations
64 for riparian ecosystem functions against water level fluctuated disturbance.

65

66 **Keywords:** Three Gorges Reservoir, non-destructive method, *Cynodon dactylon*, gap fraction,
67 seasonal change, general model

68

69 **Abbreviations**

70 AGB: Vegetation aboveground biomass

CC: Canopy cover

71 H: Canopy height

LAI: Leaf area index

72 MS: May to September

SV: Seasonal growth effect variable

73 TGR: Three Gorges Reservoir

VIF: Variance inflation factor

74 V_{CC} : Volume related variable calculated via $H \times CC$

75 V_{LAI} : Volume related variable calculated via $H \times LAI$

76

77

78

79 **1. Introduction**

80 The riparian zone served as an ecotone between terrestrial and aquatic ecosystems and has
81 often been suggested to play a central role in determining the vulnerability of natural and human
82 systems to environmental changes (Capon et al., 2013; Nilsson et al., 1997). During the past
83 decades, ecosystem functions of vegetation coverage in a riparian zone have been recognized,
84 such as forming wildlife habitats and corridors, providing food for aquatic and riparian biota,
85 stabilizing riverbanks, and improving water quality (Husson et al., 2014). As the main energy
86 source of the riparian ecosystem, the aboveground biomass (AGB) of plant species is fundamental
87 to other relevant resources (e.g., soil nutrients) and thus, can determine whether ecological
88 processes are functioning appropriately (Raab et al., 2014).

89 In many ecosystematic studies, the most widely used biomass data is the seasonal maximum
90 AGB, because it can partly indicate the productivity of an ecosystem (Raab et al., 2014; Sala and
91 Austin, 2000; Thursby et al., 2002). It has been proposed that the seasonal maximum AGB is
92 inadequate for the description of the dynamics of an ecosystem (Fernandez-Alaez et al., 2002). A
93 collection of AGB dynamics throughout a growth season has been considered increasingly
94 important for managing ecosystems (Fernandez-Alaez et al., 2002; Paillisson and Marion, 2006),
95 modelling ecosystem processes (Hidy et al., 2012; Scurlock et al., 2002), monitoring
96 plant-ecosystem functioning (Hooper et al., 2005), and evaluating vegetation life strategies against
97 environmental changes (Castelan-Estrada et al., 2002; Jagodzinski et al., 2016). Therefore,
98 estimating the seasonal dynamics of AGB is of importance to enhance our knowledge of
99 ecological functions and management for the restoration and protection of riparian zones.

100 So far, the most accurate estimation of AGB can be achieved with the direct destructive
101 method (Marshall and Thenkabail, 2015; Redjadj et al., 2012). However, this method has two
102 inherent drawbacks: (1) it is time consuming and labor intensive (Byrne et al., 2011), but most
103 important, (2) it cannot be repeated in the same spatial location, which does not allow exact
104 seasonal monitoring of growth trajectories. Thus, an array of alternative non-destructive methods
105 has been developed over the past few decades (Redjadj et al., 2012). For example, indirectly
106 estimating the AGB by modeling the relationships between biomass and some of the biometrics
107 that are relevant to plant canopy structure (Martin et al., 2005; Pottier and Jabot, 2017). These
108 biometrics including canopy height (Martin et al., 2005; Schmer et al., 2010), canopy cover
109 (Flombaum and Sala, 2007; Zhang et al., 2016), leaf area index (LAI) (Liira et al., 2002; Rutten et
110 al., 2015), and some canopy volume related indices such as the product of height and cover
111 (Redjadj et al., 2012; Penderis and Kirkman, 2014; Pottier and Jabot, 2017).

112 Most of these studies for AGB estimation that utilize canopy structural variables focused on a
113 specific growing stage (e.g., after reaching peak biomass) during a growing season. However, so
114 far, the capabilities of those variables for estimating AGB in different growing stages along one
115 growing season have not been fully explored. This poses two questions: (1) how will the
116 performances of the corresponding AGB estimation models change along a growing season for a
117 specific variable? Furthermore, (2) which of the variable(s) could be the **most important**

118 estimator(s) for AGB throughout the growing season for a specific type of model (e.g., linear
119 regression model)? For the first question, researchers have reported that the performance of
120 models often depends on sampling dates (Ferraro et al., 2012; Virkajarvi, 1999). Martin et al.
121 (2005) compared allometric equations relating canopy height to individual biomass using data that
122 was collected on ten sampling dates in two distinct pastures and found that the estimating
123 parameter varied with sampling occasions. The authors attributed this to seasonal changes in the
124 species composition and structural characteristics of the stand (Martin et al., 2005). Using linear
125 regression for AGB estimation via rising-plate meter measurements of canopy height, Nakagami
126 and Itano (2014) found that the AGB slope against height decreased during the early season and
127 then increased towards the end of the season. They furthermore developed a novel general model
128 by incorporating sampling date variations. To the best of our knowledge however, little efforts
129 have yet been undertaken to compare the capabilities among a group of variables for AGB
130 estimation throughout an entire growing season. The question this raises is: which variable(s) are
131 the **most important** estimator(s) of AGB throughout a growing season? The answer to this question
132 will be helpful in guiding efficient sampling and modeling works in future.

133 The Three Gorges Reservoir (TGR) of China is a human-disturbed reservoir ecosystem. It was
134 shaped by the Three Gorges Dam, which is one of the largest hydropower projects in the world to
135 date (Fu et al., 2010). Since its first impound in 2003, the TGR has greatly altered the surrounding
136 terrestrial environment with the largest range of annual water level fluctuations between 145 m to
137 175 m (after 2010), finally forming more than 300 km² of riparian zone (Zhang, 2008). Unlike
138 other natural riparian ecosystems in the same climatic zone, the riparian zone that surrounds the
139 TGR experiences low-water-level in summer but high-water-level in winter because of the
140 artificial water level regulation. This type of dry-wet cycle causes heavy stress on the riparian
141 ecosystem, resulting in severe habitat degradation (Su et al., 2013; Chen et al., 2015). For example,
142 the vegetation (predominantly herbaceous plants) grown in summer will be submerged and died
143 out in winter.

144 *Cynodon dactylon* (L.) Pers. (i.e., Bermuda grass) is an endemic grass within the riparian zone
145 of the TGR that forms both aboveground stolons and belowground rhizomes (Dong and Kroon,
146 1994). Since the species has a strong capability to adapt to the dry-wet cycle disturbance of the
147 degraded riparian habitat, it quickly became a pioneer and the most dominant plant species in the
148 riparian ecosystem of the TGR (Chen et al., 2015; Liu et al., 2011). Consequently, *C. dactylon*
149 plays a crucial role for ecosystem services by providing productivity, habitat, soil conservation,
150 and riparian reinforcement, as well as protecting the water quality (Liu et al., 2011). Estimating
151 the seasonal dynamic AGB of *C. dactylon* communities is thus, key for understanding riparian
152 community succession, for monitoring riparian zone restoration processes, and for managing the
153 reservoir ecosystems of the TGR (Byrne et al., 2011; Sala and Austin, 2000). Moreover, the
154 evaluating of various canopy structural variables' capabilities in estimating seasonal AGB is also
155 an urgent need as stated before. Therefore, this study targeted on the *C. dactylon* communities and
156 aimed to: (1) to find the most important factor that impacts on AGB in different season, and (2) to

157 develop a best model that can estimate the AGB throughout the growing season with multiple
158 structural variables. Results are expected to be helpful in conducting efficient seasonal AGB
159 sampling and modeling works in the future for different research conditions and objects.

160

161 2. Methods

162 2.1 Study area

163 The study area is located in the upper-mid section of a primary tributary (named Pengxi River)
164 of the Yangtze River, China (Fig. 1). The area has a humid subtropical monsoon climate,
165 characterized by warm winters and hot summers. The mean annual temperature is 18.6 °C and the
166 mean annual precipitation is 1300 mm. The slope in the area is low and the main soil type is
167 purple soil. Prior to the formation of the TGR, it had a long history of agricultural reclamation
168 with major land use types of paddy fields and dry farmland. After 2003, lands were abandoned and
169 riparian zones formed due to the sharp water-level fluctuations of the TGR. Since then, the
170 riparian zone entered a succession process. This area is suggested as a typical region that reflects
171 the impact of the TGR, and various studies have covered the region related to different topics
172 about the riparian zone in the TGR (Chen et al., 2012; Wang et al., 2014). Dominant plant species
173 in the riparian zone are *Cynodon dactylon*, *Echinochloa colonum*, *Xanthium sibirium*, and *Setaria*
174 *viridis*. Among these, *C. dactylon* and *E. colonum* are largely distributed throughout lowland area
175 (147 – 165 m), and the rest are predominantly distributed throughout highland area (165 – 175 m)
176 (Chen et al., 2012; Wang et al., 2014) (Fig. 1). In the lowland area, the *C. dactylon* communities
177 are almost mono-species communities which were targeted in the study.

178

179 ##### Fig. 1 is about here #####

180 2.2 Field sampling methods and data processing

181 2.2.1 Field sampling

182 Based on earlier field investigations of species distribution and practical accessibility of
183 sampling sites, five sampling sites (A-E in Fig. 1c) were selected. The places of those sites have
184 been tested (the results were not shown) having no significant effect on the modeling we
185 conducted in the Section 2.3. A maximum of four quadrats (1 × 1 m) per site were sampled for the
186 *C. dactylon* community, while the number could be reduced to two in one site according to
187 different field conditions and workloads during sampling time. During the growing season of *C.*
188 *dactylon* (May to September) in 2016, we conducted nine field samplings on May 30-31, Jun.
189 12-13, Jun. 21-22, Jul. 1-2, Jul. 10-11, Jul. 20, Aug. 16-17, Sep. 6-7, and Sep. 22-23, respectively
190 (Fig. 1d and Fig. 2). The locations of the quadrats at the different sampling dates were almost
191 spatially identical, i.e., a quadrat collected on one sampling date was placed very close to that of
192 the previously sampled within a distance less than 10 m.

193 At each quadrat three sampling steps were conducted: Firstly, canopy heights at four corners
194 were measured via meter stick and their mean value was recorded as the canopy height. Secondly,
195 the ACCUPAR LP-80[®] ceptometer was utilized to measure the canopy gap fraction (a variable

196 used to further calculate canopy cover) and LAI (Fig. 2c and 2d). The setting parameters of the
197 instrument for each measurement were identical to maintain the consistency. In one measurement,
198 the canopy gap fraction and LAI are automatically calculated by the instrument after measuring
199 photosynthetically active radiation at both above and below (near ground) canopy in a same
200 direction (Decagon, 2010). This measurement was repeated 2-4 times in different directions to
201 reduce the directional uncertainties. For a specific quadrat, the mean values of recorded gap
202 fraction and LAI were used in our study. Thirdly, one fourth of aboveground plants in a quadrat
203 (0.5×0.5 m) were clipped and weighted. Thereafter, a part of the clipped plants (generally less
204 than 300 g) were randomly chosen, weighted, and contained in a cloth bag for later drying. In lab,
205 all collected plant samples were dried at 80 °C for 48 hours, weighted, and the dry AGBs were
206 retrieved in a unit of g/m^2 .

207

208 2.2.2 Data processing

209 According to the field sampling as mentioned above, five canopy structural variables and a
210 seasonal growth effect variable were used as candidate estimators to estimate AGB. The variables
211 and their corresponding explanations are presented below:

- 212 • **Canopy height (H)**, a canopy structural variable with values > 0 .
- 213 • **Canopy cover (CC)**, a canopy structural variable with a value ranging between 0 and 1. This
214 could indicate the horizontal distribution of foliage in a canopy. It was calculated via one
215 minus the gap fraction, which was directly measured with an ACCUPAR LP-80[®] ceptometer
216 (see above). This was done because the gap fraction was often considered as a variant of the
217 canopy cover and equal to the one minus vertically measured cover (Liu and Pattey, 2010).
- 218 • **LAI**, a canopy structural variable with a value > 0 . This could indicate the inner distribution
219 density of foliage in a canopy (Liira et al., 2002; Rutten et al., 2015).
- 220 • **V_{CC}**, a canopy related variable derived from the equation: $V_{CC} = H \times CC$.
- 221 • **V_{LAI}**, a further canopy volume related variable derived from the equation: $V_{LAI} = H \times LAI$.
- 222 • **SV**, a seasonal growth-effects variable. This was involved in this study to explore the
223 seasonal growth effects on AGB estimation. SV of a quadrat is defined as the log-transformation
224 (base 2) of growing days (i.e., the days after the first date on which a quadrat was exposed to the
225 air due to declining water level (Fig. 1d)). The log-transformation process adopted here is mainly
226 based on the understanding that *C. dactylon* could grow fast during the early growing season,
227 while then slowing down during the mid and end of the growing season (see Appendices Fig.
228 A.1).

229 The response variables of the developed models were the log-transformation (base 2) of the
230 raw AGB. This is because the raw AGB have often been suggested as inherently non-linear and
231 could thus be log-transformed to facilitate linear model construction (Thursby et al. 2002, Elzein
232 et al. 2011, Marshall and Thenkabail 2015). We tested numerous different base values for
233 log-transformation and found base 2 to be more suitable for our study. In addition, we also
234 calculated the bulk density for each sample quadrat to explore the reasons of changing the **most**

235 **important** variables in predicting the AGB. Similar to the definition by Zhang et al. (2016), the
236 bulk density in this study is the ratio of $\log_2(\text{AGB})$ to volume related indexes (either V_{CC} or V_{LAI}).

237 ##### Fig. 2 is about here #####

238 2.3 Modeling process

239 To simplify analysis, this study considered linear regression modeling only. The modeling
240 was conducted for individual sampling dates using their own respective collected samples and the
241 whole growing season using all collected samples combined. According to the study objects, we
242 conducted univariate linear regression modeling to explore **the most important estimator** of AGB
243 for different sampling dates throughout one growing season of *C. dactylon* communities. This
244 modeling means that only one variable was adopted in a linear regression. Therefore, for each
245 sampling date, there were six established univariate linear regression models. However, only the
246 variable that established the model with the maximum coefficient of determination (R^2) or the
247 lowest mean squared error (MSE), was considered as the **most important** estimator (Zhang et al.,
248 2016). It is worth to note that the selected **most important** estimator cannot guarantee that the
249 corresponding univariate model is the optimal one (i.e., with the highest accuracy and robustness)
250 for estimating the AGB, since joint effects of different variables were not taken into account in the
251 modeling. Therefore, a best subsets regression method was adopted to select the best models to
252 estimate AGB in different sampling dates throughout the growing season of *C. dactylon*
253 communities. This method can automatically choose the “best subset” model from all the (linear
254 regression) possible models, which contain a specific number of explanatory variables via criteria
255 of Akaike Information Criterion (AIC) (Akaike, 1974). In our study, the number of variables
256 ranges from one to five. Therefore, there were five output “best subset” models for a specific
257 sampling date. The selected final best model among all five candidate models was then manually
258 selected by comparing both their ΔAIC and coefficients’ variance inflation factor (VIF, identify
259 collinearity among explanatory variables (Kutne et al., 2004) values. The smaller the ΔAIC
260 (normally < 4) and VIF (normally < 5), the better the model (Burnham and Anderson, 2004). The
261 goodness of fit in regression models was expressed as R^2 , which can be interpreted as an explained
262 variation. Moreover, leave-one-out cross validation was performed on these selected models to
263 evaluate robustness of the models with regards to their prediction error (i.e., mean square error,
264 MSE_{CV}) (Elzein et al., 2011). Plots and Pearson’s linear correlations of observed and predicted
265 AGB values further illustrate the accuracy of predictions. All regression analyses were conducted
266 via linear regression function, using the XLStat add-in statistical software (Version 2014.5.03) for
267 Microsoft Excel.

268

269 3. Results

270 3.1 Descriptive analysis of samples

271 Due to relatively small sample size or invalid measurements, three of nine sampling times
272 during the growing season were eliminated in the regression analysis (i.e., on Jun. 20, Aug. 16-17,
273 and Sep. 6-7) (Table 1). For the whole sampling season (MS in Table 1), the average AGB > 1000

274 g/m² and CC > 0.9 associated with a LAI around 4.45, indicated that *C. dactylon* communities
275 within the study area were in high-density cover (Table 1). Generally, the AGB during the
276 growing season followed an increasing trend from the lowest on May 30-31 (737 ± 429 g/m²), up
277 to half of the highest on Sep. 22-23 (1404 ± 481 g/m²). The result means that the AGB of *C.*
278 *dactylon* communities were accumulated throughout the entire growing season. A fast increase in
279 AGB appeared before Jul. 10-11, indicating that the monthly net primary productivity during this
280 period is the highest during the entire growing season. Apart from AGB, H, LAI, and CC
281 generally followed increasing tendencies. All these measurements suggest that the cover of *C.*
282 *dactylon* communities was getting increasingly higher (or thicker) from May to September in
283 2016.

284

285 ##### Table 1 is about here #####

286

287 3.2 The *most important* estimators for AGB estimation throughout the growing season

288 Table 2 shows regression coefficients of models for estimating AGB (log-transformed) and
289 using six explanatory variables. For a specific variable, different fitted parameters for different
290 sampling dates were found. Taking slope (*a* in Table 2) as an example, the values for one variable
291 varied considerably throughout the growing season. The slopes of most of the variables generally
292 followed an increasing (or decreasing, depending on variable type) trend at the beginning (before
293 Jun. 12-13 and Jun. 21-22), followed by a turnover. Furthermore, no variable was detected as the
294 *most important* estimator of AGB for all sampling dates throughout the growing season. CC and
295 V_{LAI} were selected as the *most important* estimators for more sampling dates compared to others.
296 CC was considered as *the most important* estimator for May 30-31 and Jun. 12-13, because the
297 models that were established with it have the highest *R*² and the lowest MSE_{CV} compared to all
298 other variables for the same sampling date (*R*² = 0.83, MSE_{CV} = 0.24, and *r* = 0.91 for May 30-31;
299 and *R*² = 0.63, MSE_{CV} = 0.34, *r* = 0.79 for Jun. 12-13, Table 2 and Fig. 3). During the mid and end
300 of growing season (Jul. 10-11 and Sep. 22-23) however, V_{LAI} was detected as the *most important*
301 estimator of AGB. The resulting models can provide the highest *R*² and lowest MSE_{CV} (*R*² = 0.78,
302 MSE_{CV} = 0.06, and *r* = 0.81 for Jul. 10-11; and *R*² = 0.66, MSE_{CV} = 0.13, and *r* = 0.78 for Sep.
303 22-23, Table 2). On Jun. 21-22, V_{CC} was found the *most important* estimator of AGB. The
304 performance of its established model was acceptable with *R*² = 0.58 and MSE_{CV} = 0.25. On Jul.
305 1-2, CC was also found as the *most important* estimator of AGB among all six studied variables;
306 however, the regression model is at insignificance level (*p*-value = 0.14, not shown in Table 2) and
307 its explanation power is low (*R*² = 0.17, Table 2). This indicated that the univariate linear
308 regression is insufficient at such growing dates and more analysis might be required to improve
309 AGB estimation.

310

311 ##### Table 2 is about here #####

312

313

Fig. 3 is about here

314

315 *3.3 Best model selection throughout the growing season*

316

317

Table 3 is about here

318

319

Fig. 4 is about here

320

321 Table 3 lists the results of the best subsets regression analysis. As expected, the selected best
322 models incorporated more variables and achieved higher accuracies and robustness compared to
323 the corresponding selected univariate models for most of the growing season of *C. dactylon*
324 communities (Tables 2 and 3; Figs. 3 and 4). During the early growing season, the models relied
325 on the linear combination of CC and other variables for May 30-31 (LAI) and June 12-13 (H) have
326 improved the capabilities in the AGB estimation, in contrast to the models where only CC was
327 involved (Table 2). These improvements can be measured in terms of improved R^2 (0.05 for May
328 30-31 and 0.10 for June 12-13) and reduced MSE_{CV} (0.04 for May 30-31 and 0.07 for June 12-13).
329 On Jun. 21-22, the selected best model was identical to using the single variable modeling. It
330 means that variables other than V_{CC} added little value for the estimation of AGB for this sampling
331 date. On July 1-2, although the selected best model had a great improvement compared to the
332 corresponding univariate model, its R^2 still remained low (0.49). During the mid- and late growing
333 season (July 10-11 and Sept. 22-23), the selected best models both incorporated H and LAI
334 (Table 3).

335 In addition, the selected best general model for the entire growing season (MS) had a much
336 higher R^2 (0.72) and lower MSE_{CV} (0.21) than the corresponding single variable model (with $R^2 =$
337 0.61 and $MSE_{CV} = 0.28$, see Tables 2 and 3). Unlike the individual growing dates (except for July
338 10-11), the seasonal variable (SV) was selected by this general model (Table 3).

339

340 **4. Discussion**

341 *4.1. Plant biomass and canopy structures: the **most important** estimator*

342 Canopy structure is a key element for estimating plant AGB. For the entire sampling season,
343 CC was found to be the **most important** estimator of AGB and the developed model had an
344 acceptable performance ($R^2 = 0.61$ and $MSE_{CV} = 0.28$, Table 2). However, no variable was found
345 to be the **most important** estimator in estimating AGB for all sampling dates. During the early
346 growing season (from May 30-31 to June 11-12), CC was suggested as the **most important**
347 estimator of AGB and enabled reliable estimating performance. During this period, the riparian
348 grassland has a relatively low cover compared to the latter growing season (Table 1). This finding
349 is consistent with previous studies (Axmanová et al., 2012; Flombaum and Sala, 2007; Zhang et
350 al., 2016). For example, Axmanová et al. (2012) reported relatively tight correlations between
351 cover and biomass when the cover is low in sparse vegetation communities; however, the authors

352 reported poor correlations when vegetation cover was in high density. During the mid and late
353 growing season (July 10-11 and Sep. 22-23), the V_{LAI} became the **most important** estimator of
354 AGB (Table 2). Two of the key questions related to the above findings are: (1) why is CC rather
355 than related variables the **most important** estimator of AGB during the early growing season of *C.*
356 *dactylon* communities, as the volume related variables are always considered to contain more
357 structural information of plant communities; and (2) why is the V_{LAI} rather than V_{CC} the **most**
358 **important** estimator of AGB towards the end of the growing season, as both of them are volume
359 related variables.

360 Theoretically, a volume related variable correlates linearly with AGB when the
361 corresponding bulk density is constant (Zhang et al., 2016). In this study, however, the bulk
362 density of the sampling quadrats variation largely during the early growing season, and decreased
363 after that (Fig. 5). This may due to the large variation of community canopy structure in the early
364 growing season, which decreased after that (Fig. 6 and Fig. 2). This suggests that in the early
365 growing season, the large variation of bulk density resulted in less predictabilities of volume
366 variables (both V_{LAI} and V_{CC}) in estimating AGB. Similar to the findings reported by other authors
367 (e.g., Axmanová et al., 2012; Ni-Meister et al., 2010), the CC could be more suitable to estimate
368 AGB during the early growing season since mean plant densities were relatively low (Fig. 2 and
369 Table 1). Thus, this suggests that in data sets that are collected during the early growing season in
370 a riparian environment, CC presents reasonably reliable estimates of biomass that are easy to
371 obtain. At the end of the growing season in *C. dactylon* communities, the variation of bulk
372 densities is relatively small, suggesting that a volume variable (V_{LAI} or V_{CC}) could correlate highly
373 with AGB and be more suitable to be used for estimating AGB. Although two volume related
374 variables exist (V_{CC} and V_{LAI}), our analysis suggests that V_{LAI} could be more suitable than V_{CC} for
375 the AGB estimation. This may be due to the general understanding that LAI contains more inner
376 structural information (such as layer density) than CC at the end of the growing season of *C.*
377 *dactylon* communities, when the communities had become very dense (see Appendices Fig. A.2).
378 As demonstrated in previous studies, *C. dactylon* is a stoloniferous and rhizomatous grass species
379 with high growth rates when resources are available (Dong and Kroon, 1994). Its stolons extend to
380 seek more radiance under the dense canopy cover (De Abelleira et al., 2008). As a consequence,
381 towards the end of the growing season, the canopy structure of *C. dactylon* communities often
382 contains two distinct layers: a highly overlapping stolon layer on the ground surface and erect
383 branches above the stolon layer (see Appendices Fig. A.2) (Ecoport, 2012). Since CC of a canopy
384 has a fixed upper limit (i.e., 1), it moves toward saturation, while the community cover is getting
385 higher during the growing season in September (Table 1). In this case, this could lead to
386 misinterpretation in density and structurally diverse plant populations, and thus provide less useful
387 information about canopy structural changes (Axmanová et al., 2012). However, the LAI is
388 essentially a variable with no upper limit value, and thus can indicate more information of
389 structural changes at the same condition (Fig. 6).

390 ##### Fig. 5 is about here #####

391

392

Fig. 6 is about here

393

394

395

396

397

398

399

400

401

402

403

4.2. Optimal biomass estimated models along the growing season: the joint effects

404

405

406

407

408

409

410

411

412

413

414

415

416

417

418

419

420

421

422

423

424

425

426

427

428

429

All this suggests that the canopy structural characteristics of a stand are important factors that determine the change of the **most important** AGB estimator (Martin et al., 2005). It is impractical to find a universal predictor that can be applied to all growing season of plants, given that the canopy structures constantly change like for the investigated *C. dactylon* in this study. Although the CC has been suggested as the universal **most important** estimator of AGB for the whole growing season in this study, the model on which this is based is not reliable enough to put it into practice due to its relatively low R^2 (0.61). Therefore, when other AGB estimation models are applied in practice, more attention needs to be paid on the sampling dates and plant structure characteristics on which these models were based (Martin et al., 2005; Zhang et al., 2016).

Although most of the models that were established on selected the **most important** estimators can obtain reliable accuracies for estimating AGB (Table 2), they may not be optimal models since joint effects of the studied variables were not considered. After conducting best subsets regression, the overall performance of the newly built best models significantly improved, compared to the univariate models. For instance, the selected best models explained an additional 11% in AGB variance on average (Table 3). Consequently, the best-selected models in consideration of the joint effects of variables (except for June 21-22) could provide accurate estimations of AGB dynamics for different growing dates. Generally, higher accuracy could be achievable by incorporating more variables (but with less multicollinearity) to the univariate models (Fleming et al., 2014). Recently, many studies have found that some canopy properties such as the green index and the red edge reflectance could be easily measured via remote sensing techniques and can provide useful information for the estimation of grassland AGB (Byrne et al., 2011; Chen et al., 2009; Marshall and Thenkabail, 2015). Thus, these types of variables could be incorporated to develop non-destructive methods in estimating the AGB of grassland communities of riparian zones in the future. Moreover, the best model related variables could also be obtained via new generation remote sensing technology (Ni-Meister et al., 2010; Poeschel et al., 2014; Richter et al., 2012). Thus, the selected best model could be further developed and generalized into larger scale applications in the riparian zones of the TGR and for similar areas.

The selected best general model for an entire growing season provides a relatively good performance in estimating the AGB ($R^2 = 0.72$ and $MSE_{CV} = 0.21$, Table 3). It would be very useful to estimating AGB via model interpolation during some other sampling dates, in which samples were not collected or in which the established individual models lacked reliability, such as for June 21-22 and July 1-2 in this study. In the model, CC, H, and SV were selected. These variables represent the horizontal canopy structure (CC), the vertical canopy structure (H), and seasonal growth effects (SV) of *C. dactylon* communities. In many previous studies, canopy structural variables were often considered to be important estimators of AGB; however, the

430 seasonal growth effects were considered less in these models (Hidy et al., 2012; Martin et al.,
431 2005; Redjadj et al., 2012). In this study, the SV was found to be helpful in improving AGB
432 estimation. This result is in accordance with the work conducted by Nakagami and Itano (2014), in
433 which they suggested that a general model considering the sampling date effect in an appropriate
434 way could be useful to improve the performance of an AGB estimation model. Although our
435 developed general models are specific for one dominant species in a riparian environment, the
436 methods we developed for the general model should be applicable to herbaceous species in other
437 environments, where plant growth follows distinct canopy structures throughout the growing
438 season.

439 Both the univariate and the multivariate models for July 1-2 have rather low R^2 compared to
440 models for other growing season ($R^2 = 0.17$ and 0.49 , respectively, Tables 2 and 3). Two possible
441 reasons could explain this result: Firstly, the difference of sampling condition, in terms of the
442 distinction of water and soil attached to plants, between quadrats was distinct. Heavy rain
443 preceded the field sampling of July 1st. It resulted in considerable amounts of mud attached to the
444 plants (when clipping), thus causing some uncertainties in measuring AGB, CC, and LAI for the
445 quadrats on that day, given that the ACCUPAR LP-80 equipment is easily affected by the water
446 content (Decagon, 2010). On July 2, however, some water on plants and ground had dried due to
447 sunny weather. Secondly, the values of collected samples on June 1-2 were convergent as their
448 standard deviations were relatively low, e.g., AGB of 273 g/m^2 , H of 8 cm, LAI of 0.39, and CC
449 of 0.04 (Table 1). Those concentrated sampling data can undermine the predictability of the
450 regression model. This might be caused by a new sampler (a postgraduate student with less
451 training) on that sampling date, who tended to select quadrats with high density cover and omitted
452 to take the gradient effects into account during sampling.

453

454 4.3. Limitations

455 The *C. dactylon* communities investigated in the riparian zone of the TGR were focused. They
456 are mainly distributed in lowland with elevations roughly below 165 m (Chen et al., 2012).
457 However, other communities (e.g., *Xanthium sibiricum* Patr, and *Setaria viridis* (L.) Beauv) were
458 mainly found between 165 m to 175 m and were not considered here due to their relative low
459 evenness along the TGR drawdown zone and the limited number of sampling quadrants (not
460 shown in this study). More field work is required to estimate the AGB of those communities by
461 obtaining a sufficient number of samples over the next few years. Moreover, although an
462 approximate 10-day interval field sampling was tried to be conducted throughout the growing
463 season, they were still unable to be guaranteed after July 20 due to some unforeseen factors such
464 as rising water level and intolerable hot weather during August (see Fig. 1d). Nevertheless, the
465 valid sampling dates still covered the early (May and June), middle (July), and end (September) of
466 the growing season of *C. dactylon* communities. Therefore, the findings of this study are also
467 expected to be helpful for sampling work, aimed at understanding seasonal AGB dynamics in
468 future.

469

470

471 **5. Conclusion**

472 Seasonal AGB dynamics of pioneer plant species during early succession is a key indicator
473 for both planning and monitoring of ecosystem restorations. This study focused on one dominant
474 plant pioneer species in the TGR riparian zone: *C. dactylon*. We explored the capabilities of five
475 canopy structure variables and one seasonal growth effects variable to estimate the AGB of the
476 species along different dates throughout the growing season. Our results indicate that the studied
477 canopy structural variables can be applied for estimating the AGB with reasonable accuracy and
478 robustness. However, the seasonal change of canopy structure indicates that there is no variable
479 that can be the **most important** AGB estimator throughout the entire growing season. CC was
480 found as the best estimator during the early growing season, and V_{LAI} became **the most important**
481 for the middle and the end of the growing season. The joint effects of multiple structural variables
482 were also demonstrated to be helpful in improving AGB estimation of different sampling dates. A
483 reliable general model for estimating AGB during the entire growing season was also developed
484 with the contribution of SV. The selected **most important** estimators and models of AGB
485 estimating can be used as indicators for monitoring ecosystem productivity, succession, and
486 restoration processes of riparian ecosystems. Given that the structural variables can be obtained
487 via current remote sensing techniques, it is recommended that the developed models can also be
488 applied for the rapid estimation of biomass in riparian zones, using remotely sensed data and that
489 they can be extended to regional scales. Furthermore, the models developed at different growing
490 dates enable time-series analysis of biomass dynamics, which is essential for assessing the
491 temporal response patterns of seasonal changes, and might provide both empirical and theoretical
492 explanations of riparian zone ecosystem functions in response to water level fluctuations in the
493 TGR. Finally, we suggest that the development of estimating models via our approach could
494 expand upon, rather than replace, the other modeling methods.

495

496 **Acknowledgements**

497 We are grateful to our postgraduate student Xinrui Fang and a local worker for their help
498 with fieldwork. We also thank the anonymous reviewers for their valuable suggestions and
499 comments. This work was supported by the National Natural Science Foundation of China [grant
500 numbers: 41501096, 41571497, and 41401051].

501

502 **References**

503 Akaike, H., 1981. A new look at the statistical model identification. IEEE T. Automat. Contr. 19,
504 716-723.

505 Axmanová, I., Tichý, L., Fajmonová, Z., Hájková, P., Hettenbergerová, E., Li, C.-F., Merunková,
506 K., Nejezchlebová, M., Otýpková, Z., Vymazalová, M., Zelený, D., 2012. Estimation of
507 herbaceous biomass from species composition and cover. Appl. Veg. Sci. 15, 580-589.

508 Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in
509 model selection. *Sociol. Methods Res.* 33, 261-304.

510 Byrne, K.M., Lauenroth, W.K., Adler, P.B., Byrne, C.M., 2011. Estimating aboveground net
511 primary production in grasslands: a comparison of nondestructive methods. *Rangeland Ecol.*
512 *Manag.* 64, 498-505.

513 Capon, S.J., Chambers, L.E., Mac Nally, R., Naiman, R.J., Davies, P., Marshall, N., Pittock, J.,
514 Reid, M., Capon, T., Douglas, M., Catford, J., Baldwin, D.S., Stewardson, M., Roberts, J.,
515 Parsons, M., Williams, S.E., 2013. Riparian ecosystems in the 21st century: hotspots for
516 climate change adaptation? *Ecosystems* 16, 359-381.

517 Castelan-Estrada, M., Vivin, P., Gaudillere, J.P., 2002. Allometric relationships to estimate
518 seasonal above-ground vegetative and reproductive biomass of *Vitis vinifera* L. *Ann. Bot.* 89,
519 401-408.

520 Chen, F., Zhang, J., Zhang, M., Wang, J., 2015. Effect of *Cynodon dactylon* community on the
521 conservation and reinforcement of riparian shallow soil in the Three Gorges Reservoir area.
522 *Ecol. Process.* 4, 3.

523 Chen, J., Gu, S., Shen, M., Tang, Y., Matsushita, B., 2009. Estimating aboveground biomass of
524 grassland having a high canopy cover: an exploratory analysis of in situ hyperspectral data.
525 *Int. J. Remote Sens.* 30, 6497-6517.

526 Chen, Z.L., Yuan, X.Z., Liu, H., Bo, L.I., 2012. Effects of water level fluctuation on plant
527 communities in the littoral zone of the Three Gorges Reservoir. *Resources & Environment in*
528 *the Yangtze Basin* 21, 672-677 (in Chinese with English abstract).

529 De Abelleira, D., VerdÚ, A.M.C., Kruk, B.C., Satorre, E.H., 2008. Soil water availability affects
530 green area and biomass growth of *Cynodon dactylon*. *Weed Res.* 48, 248-256.

531 Decagon, 2010. AccuPAR PAR/LAI Ceptometer Model LP-80, Version 10 ed. Decagon devices,
532 Inc., Pullman, WA, USA.

533 Dong, M., Kroon, H.D., 1994. Plasticity in morphology and biomass allocation in *Cynodon*
534 *dactylon*, a grass species forming stolons and rhizomes. *Oikos* 70, 99-106.

535 Ecoport, 2012. Ecoport database. Ecoport.

536 Elzein, T.M., Blarquez, O., Gauthier, O., Carcaillet, C., 2011. Allometric equations for biomass
537 assessment of subalpine dwarf shrubs. *Alpine Bot.* 121, 129-134.

538 Fernandez-Alaez, M., Fernandez-Alaez, C., Rodriguez, S., 2002. Seasonal changes in biomass of
539 charophytes in shallow lakes in the northwest of Spain. *Aquat. Bot.* 72, 335-348.

540 Ferraro, F.P., Nave, R., Sulc, R.M., Barker, D.J., 2012. Seasonal variation in the rising plate meter
541 calibration for forage mass. *Agron. J.* 104, 1-6.

542 Fleming, G.M., Wunderle, J.M., Ewert, D.N., O'Brien, J.J., 2014. Estimating plant biomass in
543 early-successional subtropical vegetation using a visual obstruction technique. *Appl. Veg. Sci.*
544 17, 356-366.

545 Flombaum, P., Sala, O.E., 2007. A non-destructive and rapid method to estimate biomass and
546 aboveground net primary production in arid environments. *J. Arid Environ.* 69, 352-358.

547 Fu, B.J., Wu, B.F., Lu, Y.H., Xu, Z.H., Cao, J.H., Niu, D., Yang, G.S., Zhou, Y.M., 2010. Three
548 Gorges Project: efforts and challenges for the environment. *Prog. Phys. Geog.* 34, 741-754.

549 Hidy, D., Barcza, Z., Haszpra, L., Churkina, G., Pinter, K., Nagy, Z., 2012. Development of the
550 Biome-BGC model for simulation of managed herbaceous ecosystems. *Ecol. Model.* 226,
551 99-119.

552 Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge,
553 D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle,
554 D.A., 2005. Effects of biodiversity on ecosystem functioning: A consensus of current
555 knowledge. *Ecol. Monogr.* 75, 3-35.

556 Husson, E., Lindgren, F., Ecker, F., 2014. Assessing biomass and metal contents in riparian
557 vegetation along a pollution gradient using an unmanned aircraft system. *Water Air Soil Poll.*
558 225, 1957.

559 Jagodzinski, A.M., Dyderski, M.K., Rawlik, K., Katna, B., 2016. Seasonal variability of biomass,
560 total leaf area and specific leaf area of forest understory herbs reflects their life strategies.
561 *Forest Ecol Manag* 374, 71-81.

562 Kutne, M., Nachtsheim, C., Neter, J., 2004. Applied linear regression models. McGraw-Hill
563 Education.

564 Liira, J., Zobel, K., Mägi, R., Molenberghs, G., 2002. Vertical structure of herbaceous canopies:
565 the importance of plant growth-form and species-specific traits. *Plant Ecol.* 163, 123-134.

566 Liu, J.G., Pattey, E., 2010. Retrieval of leaf area index from top-of-canopy digital photography
567 over agricultural crops. *Agric. For. Meteorol.* 150, 1485-1490.

568 Liu, W.W., Yang, F., Wang, J., Wang, Y., 2011. Plant species dynamic distribution in the
569 water-level-fluctuating zone of the main stream and bay of the Three Gorges Reservoir. *Plant*
570 *Sci. J.* 29, 296-306 (in Chinese with English abstract).

571 Marshall, M., Thenkabail, P., 2015. Developing in situ non-destructive estimates of crop biomass
572 to address issues of scale in remote sensing. *Remote Sens.* 7, 808.

573 Martin, R.C., Astatkie, T., Cooper, J.M., Fredeen, A.H., 2005. A comparison of methods used to
574 determine biomass on naturalized swards. *J. Agron. Crop Sci.* 191, 152-160.

575 Nakagami, K., Itano, S., 2014. Improving pooled calibration of a rising-plate meter for estimating
576 herbage mass over a season in cool-season grass pasture. *Grass Forage Sci.* 69, 717-723.

577 Nilsson, C., Jansson, R., Zinko, U., 1997. Long-term responses of river-margin vegetation to
578 water-level regulation. *Science* 276, 798-800.

579 Ni-Meister, W., Lee, S., Strahler, A.H., Woodcock, C.E., Schaaf, C., Yao, T., Ranson, K.J., Sun, G.,
580 Blair, J.B., 2010. Assessing general relationships between aboveground biomass and
581 vegetation structure parameters for improved carbon estimate from lidar remote sensing. *J.*
582 *Geophys. Res.* 115, G00E11.

583 Paillisson, J.M., Marion, L., 2006. Can small water level fluctuations affect the biomass of
584 *Nymphaea alba* in large lakes? *Aquat Bot* 84, 259-266.

585 Penderis, C.A., Kirkman, K.P., 2014. Using partial volumes to estimate available browse biomass
586 in Southern African semi-arid savannas. *Appl. Veg. Sci.* 17, 578-590.

587 Pottier, J., Jabot, F., 2017. Non-destructive biomass estimation of herbaceous plant individuals: a
588 transferable method between contrasted environments. *Ecol. Indic.* 72, 769-776.

589 Poeschel, P., Newnham, G., Hill, J., 2014. Retrieval of gap fraction and effective plant area index
590 from phase-shift terrestrial laser scans. *Remote Sens.* 6, 2601.

591 Raab, D., Rooney, R.C., Bayley, S.E., 2014. A visual obstruction method to estimate wet meadow
592 aboveground biomass in marshes of the boreal plains, Canada. *Wetlands* 34, 363-367.

593 Raab, D., Rooney, R.C., Bayley, S.E., 2014. A visual obstruction method to estimate wet meadow
594 aboveground biomass in marshes of the boreal plains, Canada. *Wetlands* 34, 363-367.

595 Redjadj, C., Duparc, A., Lavorel, S., Grigulis, K., Bonenfant, C., Maillard, D., Said, S., Loison, A.,

596 2012. Estimating herbaceous plant biomass in mountain grasslands: a comparative study
597 using three different methods. *Alpine Bot.* 122, 57-63.

598 Richter, K., Hank, T.B., Vuolo, F., Mauser, W., D'Urso, G., 2012. Optimal exploitation of the
599 sentinel-2 spectral capabilities for crop leaf area index mapping. *Remote Sens.* 4, 561-582.

600 Rutten, G., Ensslin, A., Hemp, A., Fischer, M., 2015. Vertical and horizontal vegetation structure
601 across natural and modified habitat types at Mount Kilimanjaro. *Plos One* 10: e0138822.

602 Sakamoto, Y., Kitagawa, G., 1986. Akaike information criterion statistics. Kluwer Academic
603 Publishers.

604 Sala, O.E., Austin, A.T., 2000. Methods of estimating aboveground net primary productivity, in:
605 Sala, O.E., Jackson, R.B., Mooney, H.A., Howarth, R.W. (Eds.), *Methods in ecosystem*
606 *science*. Springer New York, New York, NY, pp. 31-43.

607 Schmer, M.R., Mitchell, R.B., Vogel, K.P., Schacht, W.H., Marx, D.B., 2010. Efficient methods of
608 estimating switchgrass biomass supplies. *BioEnerg. Res.* 3, 243-250.

609 Scurlock, J.M.O., Johnson, K., Olson, R.J., 2002. Estimating net primary productivity from
610 grassland biomass dynamics measurements. *Global Change Biol.* 8, 736-753.

611 Su, X.L., Zeng, B., Huang, W.J., Yuan, S.H., Xu, S.J., Lei, S.T., 2013. The effect of winter
612 impoundment of the Three Gorges Dam: The degradation and convergence of pre-upland
613 vegetation. *Ecol. Eng.* 61, 456-459.

614 Thursby, G.B., Chintala, M.M., Stetson, D., Wigand, C., Champlin, D.M., 2002. A rapid,
615 non-destructive method for estimating aboveground biomass of salt marsh grasses. *Wetlands*
616 22, 626-630.

617 Virkajarvi, P., 1999. Comparison of three indirect methods for prediction of herbage mass on
618 timothy-meadow fescue pastures. *Acta Agr Scand B-S P* 49, 75-81.

619 Wang, Q., Yuan, X.Z., Willison, J.H.M., Zhang, Y.W., Liu, H., 2014. Diversity and above-ground
620 biomass patterns of vascular flora induced by flooding in the drawdown area of China's Three
621 Gorges Reservoir. *Plos One* 9: e100889.

622 Zhang, H., 2008. Characteristic Analyses of the Water-level-fluctuating zone in the Three Gorges
623 Reservoir. *Bulletin of Soil & Water Conservation* 28, 46-49 (in Chinese with English
624 abstract).

625 Zhang, L., Cui, G.S., Shen, W., Liu, X.S., 2016. Cover as a simple predictor of biomass for two
626 shrubs in Tibet. *Ecol. Indic.* 64, 266-271.

627

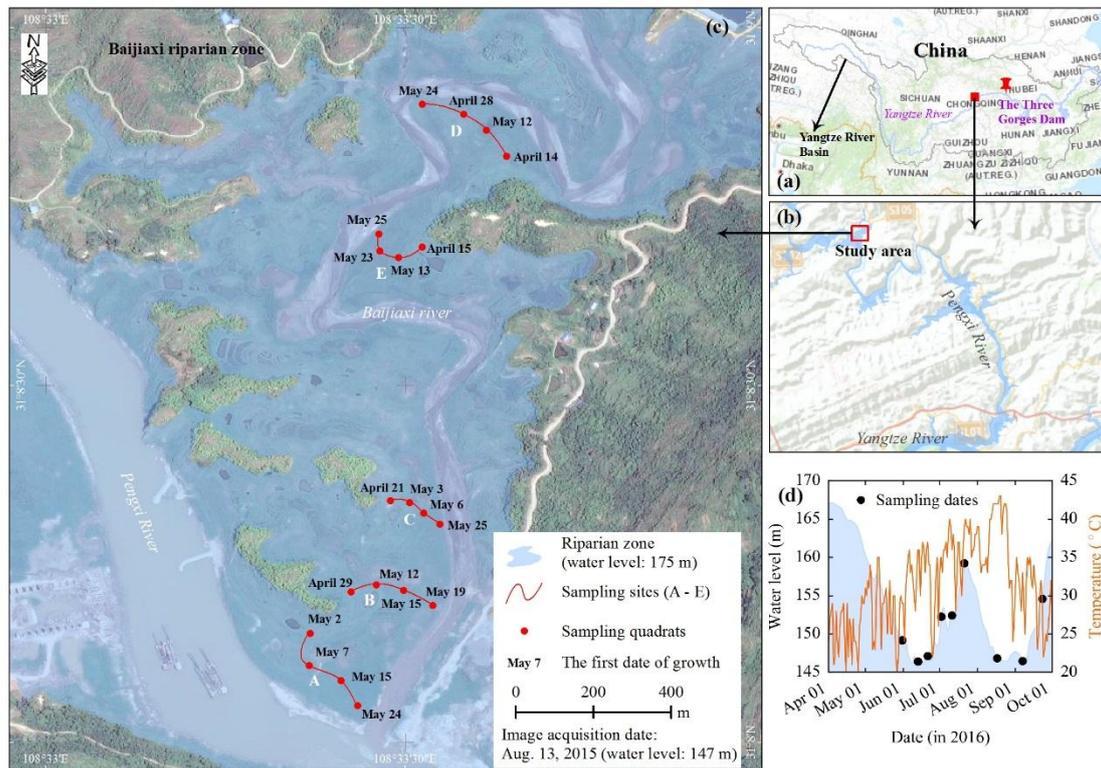


Fig. 1. Location of study area (a-b), (c) satellite image of the study area with the distribution of sampling sites, and (d) daily water level fluctuations at the Wanzhou hydrological station near the study area (data from <http://www.cxfww.cn/>), daily average temperatures, and sampling dates.

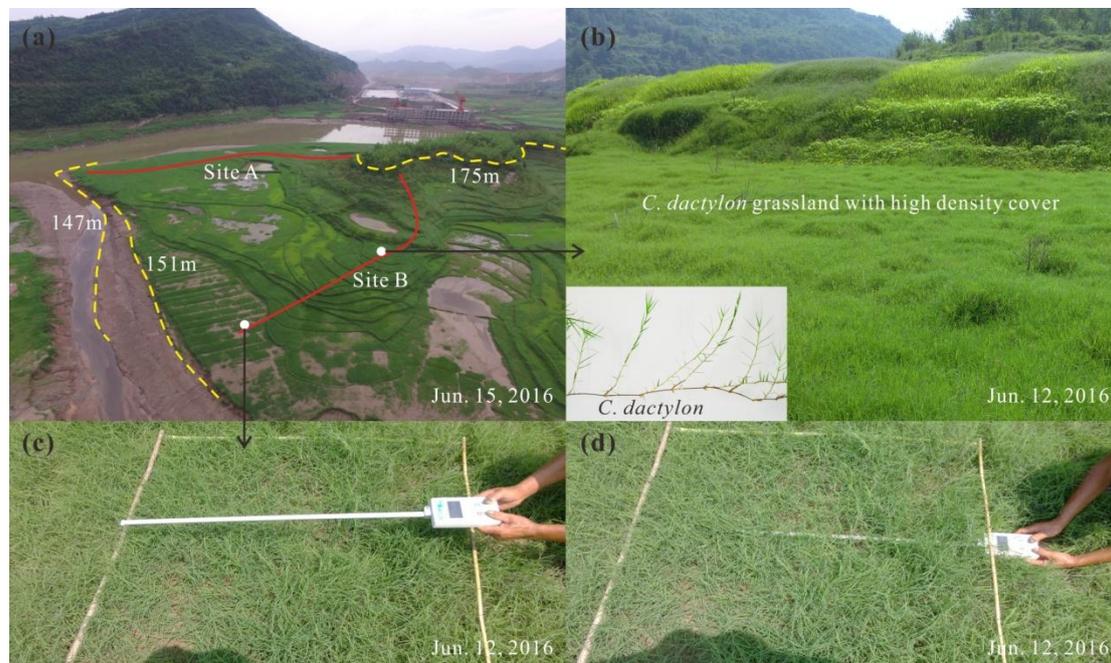


Fig. 2. Images depicting our sampling methods: (a) an overview of the sampling sites A and B (See Fig.1), (b) representative picture for a *C. dactylon* community with high density cover, (c) and (d) measuring photosynthetically active radiation both above (c) and below the canopy (d) via ACCUPAR LP-80 ceptometer.

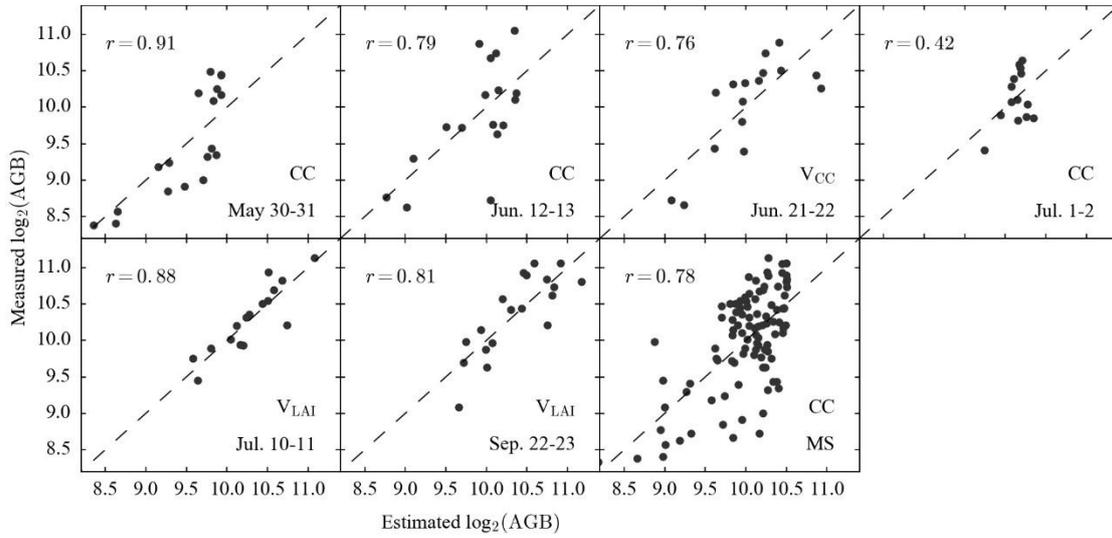


Fig. 3. Correlation coefficients (r) between the measured $\log_2(\text{AGB})$ and the estimated values via the selected best variable (i.e., the labeled variable) for different sampling dates. The dashed line marks a 1:1 ratio. MS = May 30 to Sep. 23 in 2016.

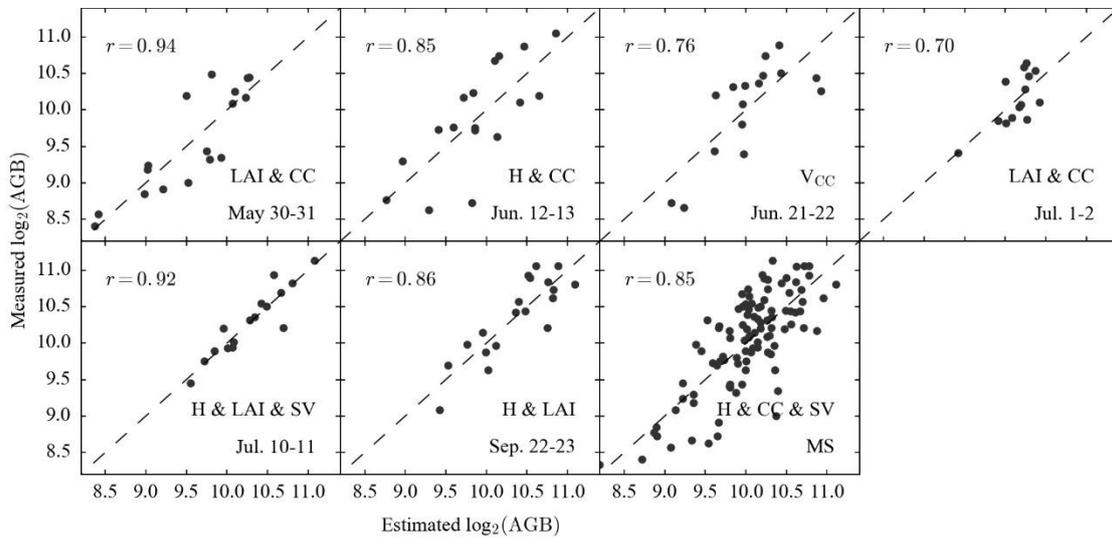


Fig. 4. Correlation coefficients (r) between the measured $\log_2(\text{AGB})$ and the estimated values via the selected best model (the involved variables were labeled) for different sampling dates. The dashed line marks a 1:1 ratio. MS = May 30 to Sep. 23 in 2016.

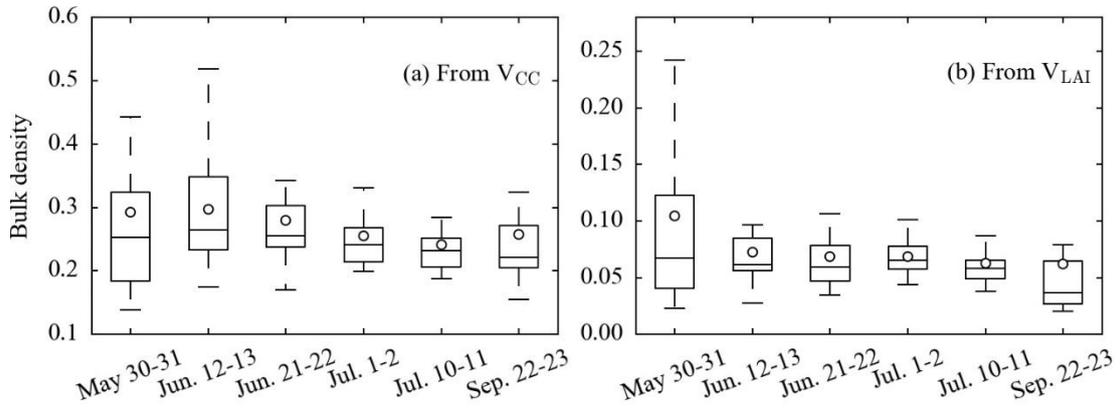


Fig. 5. Statistical distributions of the bulk densities of samples at different sampling dates. (a) Bulk density calculated from V_C and (b) from V_{LAI} . The small circle (\circ) is the mean value.

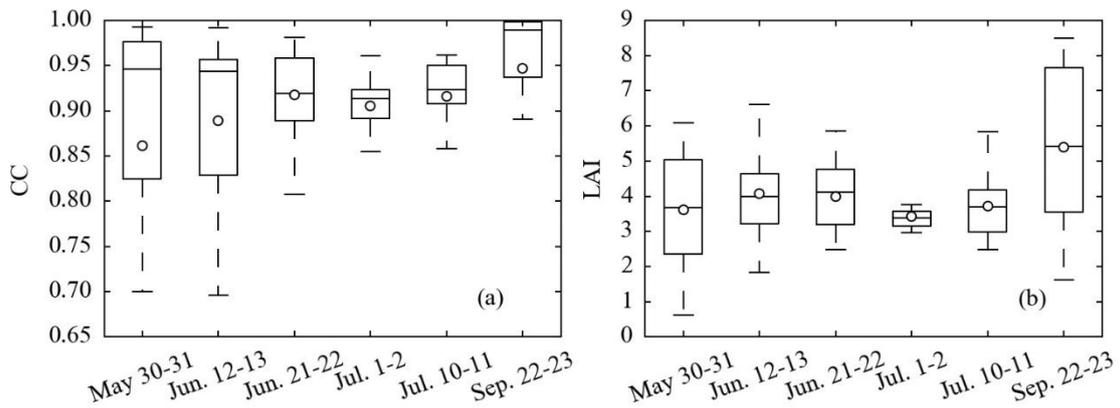


Fig. 6. Statistical distributions of the canopy cover of samples (a) and the LAI (b) at different sampling dates. The small circle (\circ) is the mean value.

Table 1. Basic statistics of *C. dactylon* community samples at different sampling dates in 2016. Sample values are shown as mean \pm standard deviation. SPD: sampling dates, NS = number of samples, AGB = aboveground biomass, H = height, LAI = leaf area index, CC = canopy cover, V_{LAI} is a canopy volume-like variable calculated via $H \times LAI$, and V_{CC} is a further volume-like variable calculated via $H \times CC$. MS = May to Sep. (i.e., all samples collected during valid sampling dates). Light gray shaded data were not applied in the regression modeling due to the relatively small number of samples or invalidity of measurements.

SPD	NS	AGB (g/m ²)	H (cm)	LAI	CC	V_{LAI}	V_{CC}
May 30-31	20	737 \pm 429	44 \pm 15	3.60 \pm 1.79	0.86 \pm 0.18	176 \pm 130	39 \pm 18
Jun. 12-13	19	979 \pm 544	40 \pm 12	4.06 \pm 1.32	0.89 \pm 0.11	171 \pm 94	36 \pm 13
Jun. 21-22	16	1144 \pm 428	43 \pm 12	3.99 \pm 0.98	0.92 \pm 0.05	172 \pm 70	39 \pm 12
Jul. 1-2	14	1171 \pm 273	46 \pm 8	3.40 \pm 0.39	0.91 \pm 0.04	156 \pm 36	41 \pm 8
Jul. 10-11	16	1314 \pm 427	48 \pm 8	3.72 \pm 0.90	0.92 \pm 0.05	176 \pm 56	44 \pm 9
Jul. 20	4	874 \pm 240	37 \pm 5	4.31 \pm 1.00	0.87 \pm 0.07	157 \pm 36	32 \pm 5
Aug. 16-17	19	1347 \pm 408	45 \pm 11	invalid	invalid	invalid	invalid
Sep. 6-7	20	1352 \pm 676	45 \pm 14	invalid	invalid	invalid	invalid
Sep. 22-23	19	1404 \pm 481	47 \pm 12	5.39 \pm 2.32	0.95 \pm 0.07	267 \pm 145	45 \pm 13
MS	104	1189 \pm 497	46 \pm 12	4.45 \pm 1.72	0.92 \pm 0.10	213 \pm 122	42 \pm 14

Table 2. Regression coefficients of models that estimate dry aboveground biomass (Y), using variables (X) of canopy height (H), canopy cover (CC), leaf area index (LAI), V_{CC} , V_{LAI} , and seasonal growth effects variable (SV) via the univariate linear model of $\log_2(Y) = aX+b$. For each sampling date, the numbers in bold depict the highest R^2 or the lowest MSE_{CV} among all six variables. Light grayed values indicate that the corresponding fitted model is insignificant with p -values > 0.05 . MS = May 30 to Sep. 23 in 2016.

Variables	Models	Sampling dates						
		May 30-31	Jun. 12-13	Jun. 21-22	Jul. 1-2	Jul. 10-11	Sep. 22-23	MS
H	a	0.039	0.051	0.040	0.008	0.033	0.032	0.040
	b	7.500	7.640	8.320	9.790	8.720	8.850	8.150
	R^2	0.288	0.461	0.561	0.035	0.372	0.512	0.331
	MSE_{CV}	0.902	0.487	0.254	0.155	0.153	0.178	0.467
	p -value	0.015	0.001	0.001	0.523	0.012	0.001	<0.001
CC	a	5.390	6.510	6.000	3.880	5.550	5.000	6.170
	b	4.580	3.890	4.500	6.620	5.250	5.600	4.330
	R^2	0.831	0.630	0.187	0.175	0.394	0.517	0.606
	MSE_{CV}	0.238	0.340	0.471	0.167	0.151	0.221	0.275
	p -value	<0.001	<0.001	0.094	0.137	0.009	0.001	<0.001
LAI	a	0.532	0.456	0.214	-0.314	0.395	0.186	0.325
	b	7.310	7.840	9.180	11.200	8.820	9.360	8.610
	R^2	0.804	0.457	0.100	0.117	0.596	0.613	0.396
	MSE_{CV}	0.271	0.512	0.473	0.129	0.100	0.143	0.428
	p -value	<0.001	<0.001	0.232	0.232	<0.001	<0.001	<0.001
V_{CC}	a	0.046	0.053	0.043	0.014	0.035	0.032	0.045
	b	7.430	7.800	8.360	9.580	8.730	8.950	8.110
	R^2	0.583	0.603	0.581	0.087	0.467	0.590	0.497
	MSE_{CV}	0.570	0.357	0.248	0.134	0.129	0.149	0.357
	p -value	<0.001	<0.001	0.001	0.305	0.004	<0.001	<0.001
V_{LAI}	a	0.006	0.007	0.007	0.007	0.007	0.003	0.005
	b	8.100	8.550	8.910	10.200	8.990	9.540	8.960
	R^2	0.607	0.503	0.479	0.001	0.776	0.658	0.426
	MSE_{CV}	0.532	0.477	0.297	0.168	0.058	0.127	0.407
	p -value	<0.001	0.001	0.003	0.924	<0.001	<0.001	<0.001
SV	a	0.457	0.074	0.868	-0.135	-0.312	-1.410	0.398
	b	7.240	9.310	5.380	10.900	12.200	20.400	7.700
	R^2	0.301	0.003	0.273	0.015	0.058	0.062	0.286
	MSE_{CV}	0.967	0.950	0.399	0.163	0.242	0.338	0.509
	p -value	0.012	0.819	0.038	0.682	0.368	0.304	<0.001

Table 3. Output of the best subsets regression. The final selected best model for an individual sampling date is marked in bold. SPD = sampling dates and NV = number of variables. MSE_{CV} = mean MSE value from the leave-one-out cross validation. “-” = no data.

SPD	NV	Selected variables (corresponding VIF value)	MSE_{CV}	MSE	R^2	AIC	ΔAIC	p-value
May 30-31	1	CC(-)	0.238	0.201	0.831	-30.161	4.842	<0.001
	2	LAI(3.92); CC(3.92)	0.199	0.153	0.879	-34.777	0.226	<0.001
	3	H(6.08); CC(2.44); V_{LAI} (9.16)	0.167	0.146	0.891	-35.003	0.000	<0.001
	4	H(57.11); LAI(8.61); CC(13.20); V_{CC} (108.95)	0.263	0.153	0.893	-33.288	1.715	<0.001
	5	H(57.12); LAI(8.68); CC(13.74); V_{CC} (109.05); SV(1.61)	0.278	0.163	0.893	-31.393	3.61	<0.001
Jun. 12-13	1	CC(-)	0.340	0.310	0.630	-20.343	3.952	<0.001
	2	H(1.36); CC(1.36)	0.269	0.241	0.729	-24.295	0.000	<0.001
	3	LAI(7.29); V_{LAI} (21.09); V_{CC} (8.40)	0.287	0.245	0.742	-23.189	1.106	<0.001
	4	H(80.44); LAI(26.05); V_{LAI} (39.38); V_{CC} (69.07)	0.338	0.259	0.746	-21.480	2.815	<0.001
	5	H(366.60); LAI(109.22); CC(92.97); V_{LAI} (221.93); V_{CC} (918.45)	0.445	0.273	0.751	-19.856	4.439	0.001
Jun. 21-22	1	V_{CC}(-)	0.248	0.198	0.581	-24.084	0.000	0.001
	2	V_{CC} (1.27); SV(1.27)	0.245	0.194	0.619	-23.590	0.494	0.002
	3	H(1.26); CC(1.21); SV(1.34)	0.254	0.202	0.634	-22.228	1.856	0.006
	4	H(320.27); CC(9.28); V_{CC} (360.45); SV(1.34)	0.297	0.207	0.655	-21.195	2.889	0.013
	5	H(529.62); LAI(53.98); CC(21.08); V_{LAI} (140.55); V_{CC} (888.40)	0.372	0.177	0.732	-23.260	0.824	0.011
Jul. 1-2	1	CC(-)	0.167	0.115	0.175	-28.481	5.515	0.137
	2	LAI(1.20); CC(1.20)	0.081	0.077	0.493	-33.310	0.686	0.024
	3	H(16.64); V_{LAI} (4.40); V_{CC} (18.98)	0.096	0.070	0.582	-33.996	0.000	0.028
	4	H(21.28); LAI(1.18); V_{CC} (22.00); SV(1.15)	0.110	0.076	0.590	-32.280	1.716	0.066
	5	H(195.11); LAI(55.35); V_{LAI} (206.24); V_{CC} (23.93); SV(1.55)	0.152	0.085	0.590	-30.286	3.71	0.141
Jul. 10-11	1	V_{LAI} (-)	0.058	0.051	0.776	-45.792	4.677	<0.001
	2	V_{LAI} (1.27); SV(1.27)	0.053	0.046	0.811	-46.562	3.907	<0.001
	3	H(1.26); LAI(1.17); SV(1.38)	0.050	0.041	0.847	-47.898	2.571	<0.001
	4	H(50.99); LAI(114.55); V_{LAI} (189.98); SV(1.99)	0.052	0.033	0.885	-50.469	0.000	<0.001
	5	H(76.41); LAI(176.34); CC(2.93); V_{LAI} (270.58); SV(2.09)	0.060	0.034	0.892	-49.561	0.908	<0.001
Sep. 22-23	1	V_{LAI} (-)	0.127	0.110	0.658	-39.976	4.885	<0.001
	2	H(1.37); LAI(1.37)	0.105	0.088	0.743	-43.386	1.475	<0.001
	3	H(6.44); LAI(21.48); V_{LAI} (36.71)	0.087	0.078	0.786	-44.861	0.000	<0.001
	4	H(6.50); LAI(24.56); V_{LAI} (39.61); SV(1.28)	0.091	0.077	0.803	-44.446	0.415	<0.001
	5	H(8.59); LAI(38.98); CC(4.13); V_{LAI} (48.79); SV(1.32)	0.105	0.083	0.804	-42.562	2.299	<0.001
MS	1	CC(-)	0.275	0.270	0.606	-134.060	32.126	<0.001
	2	H(1.24); CC(1.24)	0.238	0.227	0.673	-151.430	14.756	<0.001
	3	H(1.24); CC(1.45); SV(1.22)	0.205	0.195	0.722	-166.186	0.000	<0.001
	4	CC(2.06); V_{LAI} (3.73); V_{CC} (3.71); SV(1.23)	0.207	0.197	0.722	-164.211	1.975	<0.001
	5	H(33.94); LAI(23.58); V_{LAI} (36.68); V_{CC} (29.62); SV(1.23)	0.209	0.194	0.728	-164.598	1.588	<0.001

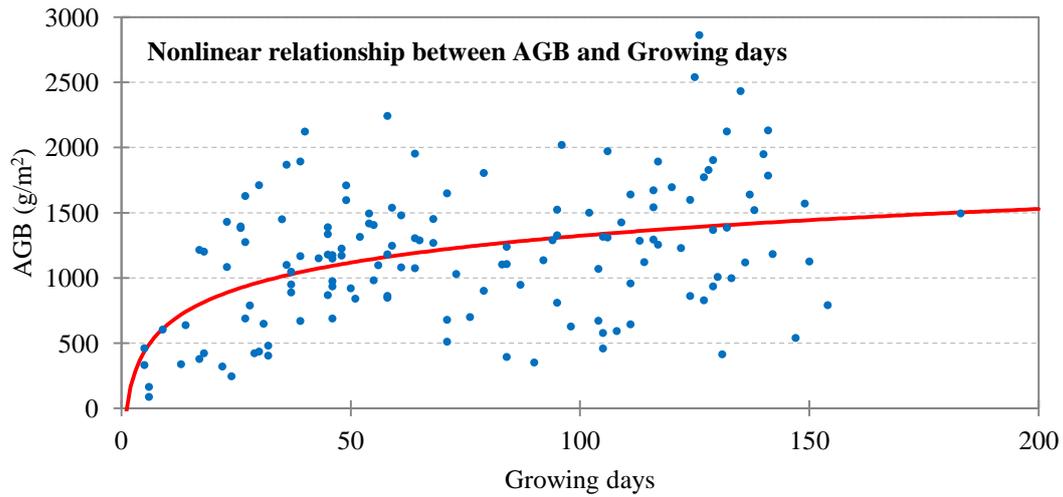


Figure A.1. Scatter plot of AGB against growing days (i.e., days after first date emerging from water in 2016) for all collected samples of *C. dactylon* communities in the growing seasons (see Table 1). It shows that the AGB was accumulated fast in the early growing seasons and then slowed down in the mid- and end- growing season. This nonlinear growing process was thus could be characterized by a logarithmic function (the red solid line). Based on this observation, the seasonal growing effect variable was defined as log-transformed (base 2) of growing days to facilitate linear AGB estimation model in this study.

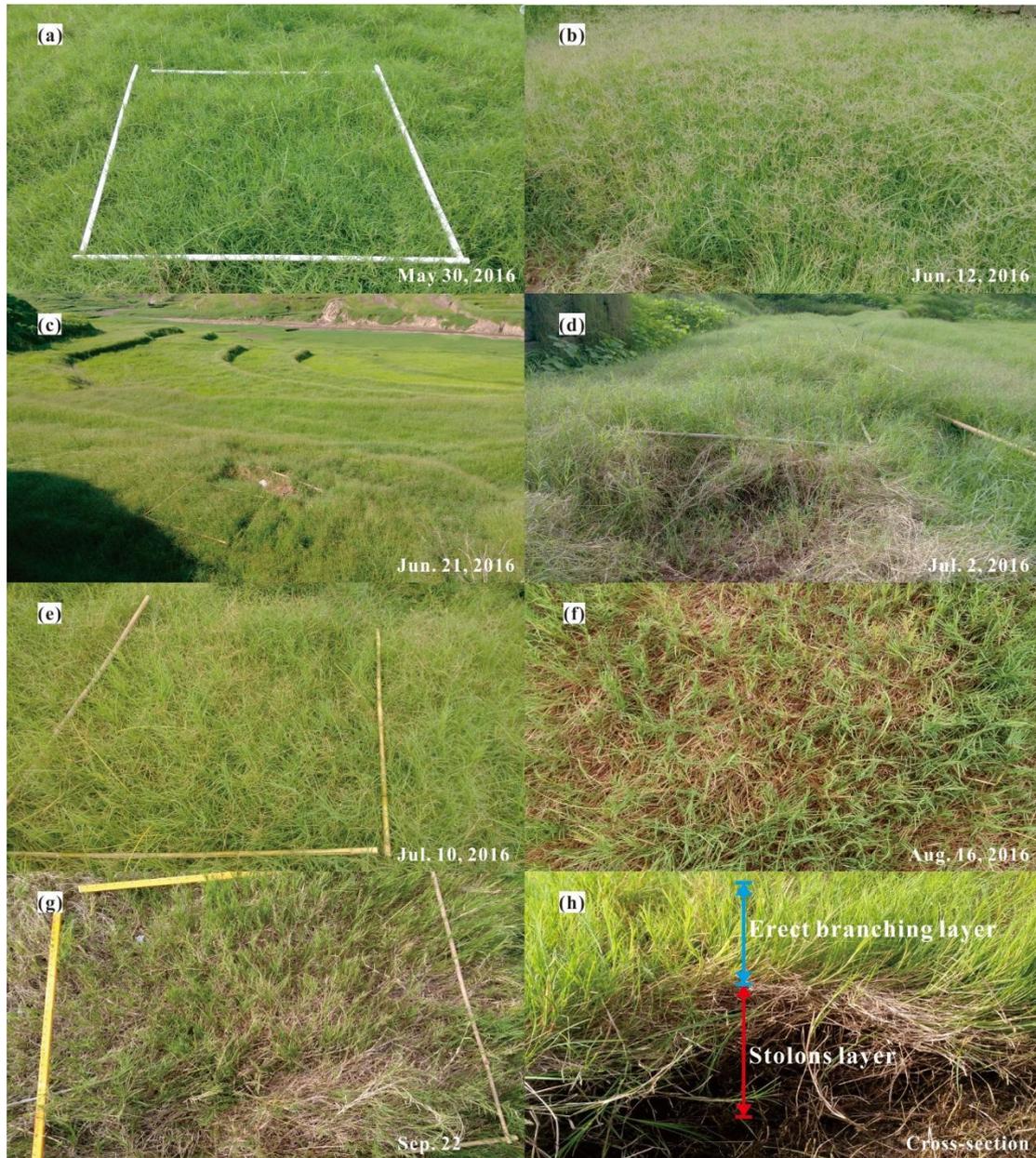


Figure A.2. (a)-(g): Growing status dynamics of *C. dactylon* community sampling quadrats in different growing seasons (from May to September). The spatial locations of these quadrats were close to each other within distance less than 10 m. (h) A cross-section view of two distinct layers of *C. dactylon* community in the end of growing season.

Fig. A.1 (Source file in PDF format)

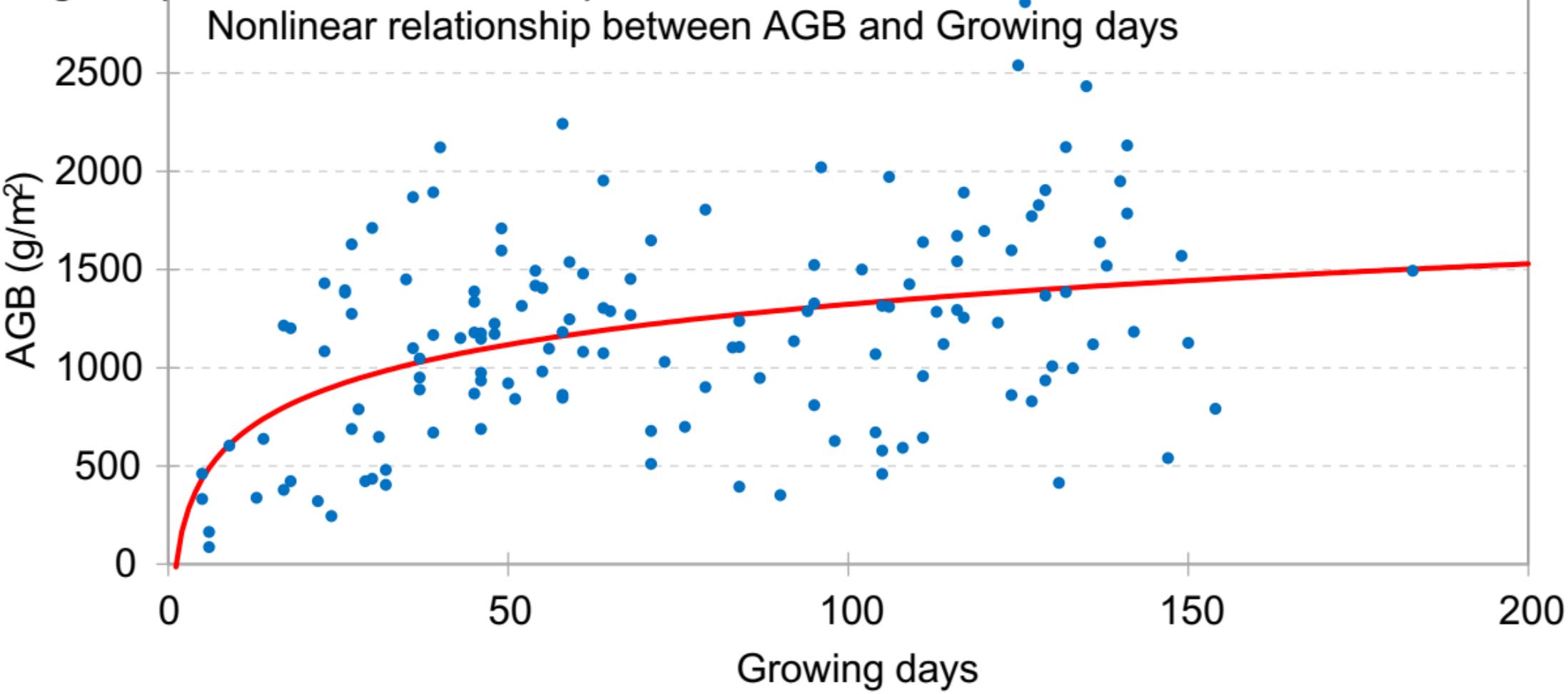


Fig. A.2 (Source file in PDF format)

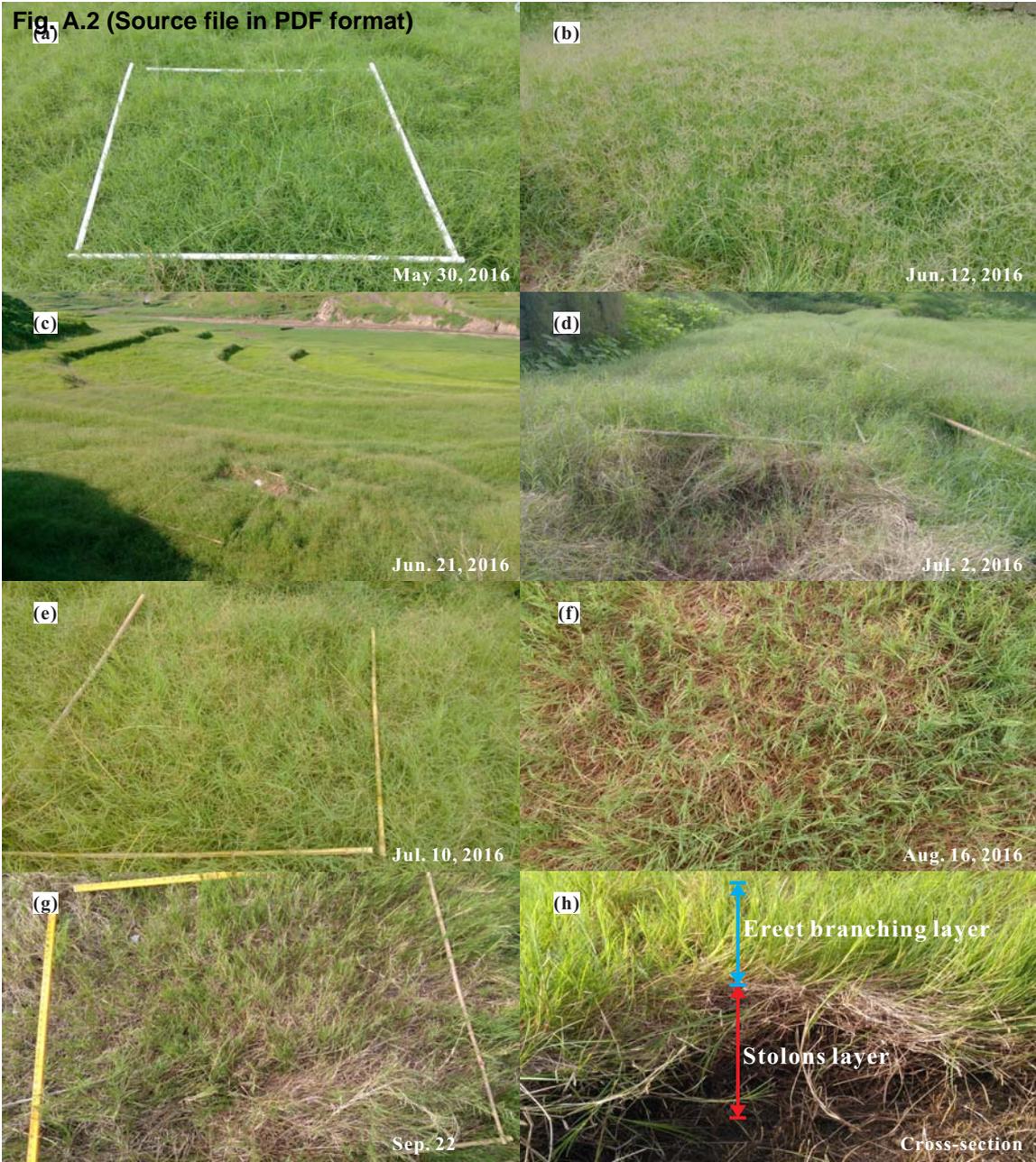


Fig. 1 (Source file in PDF format)

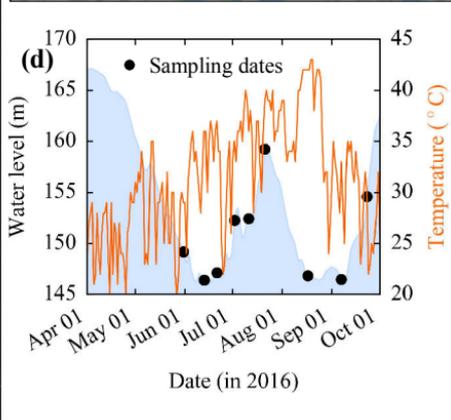
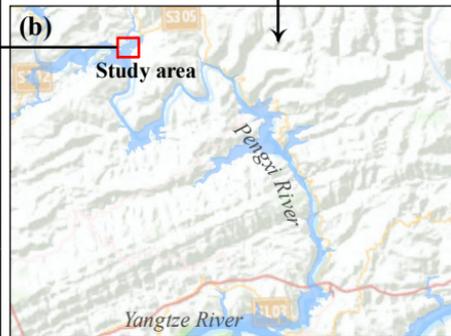
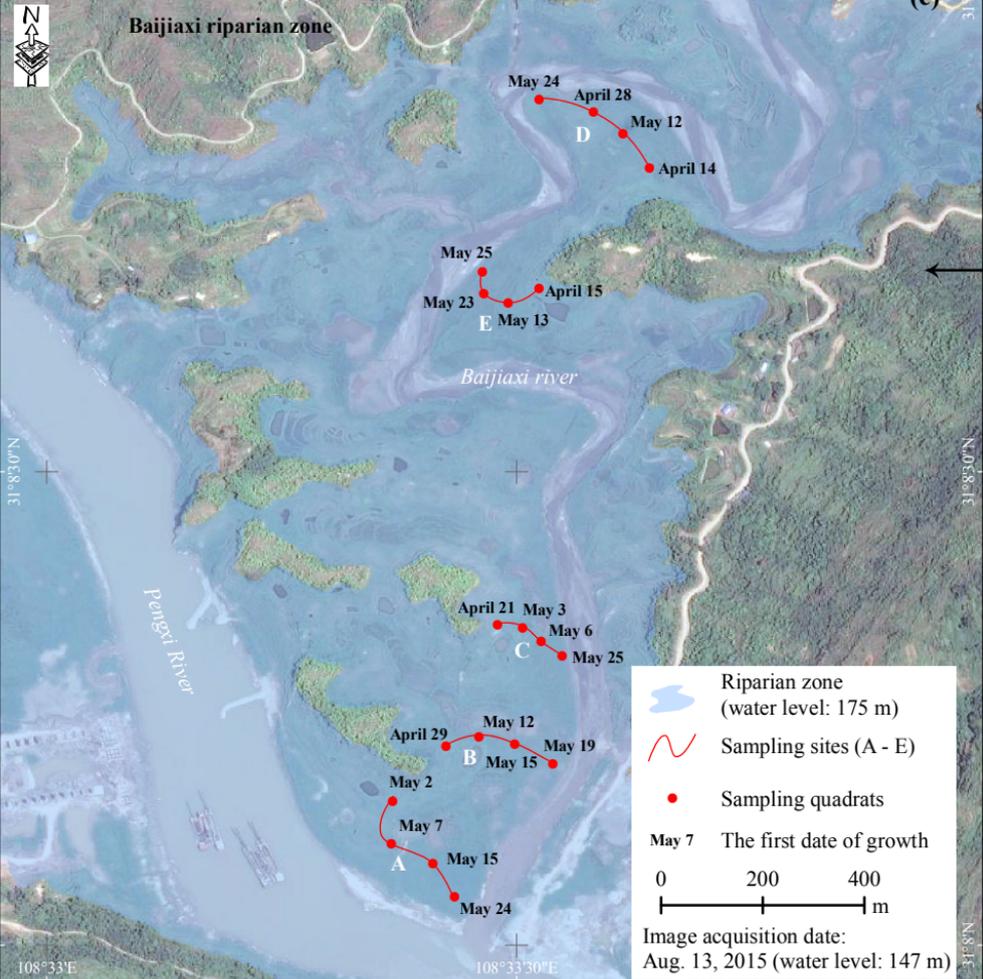
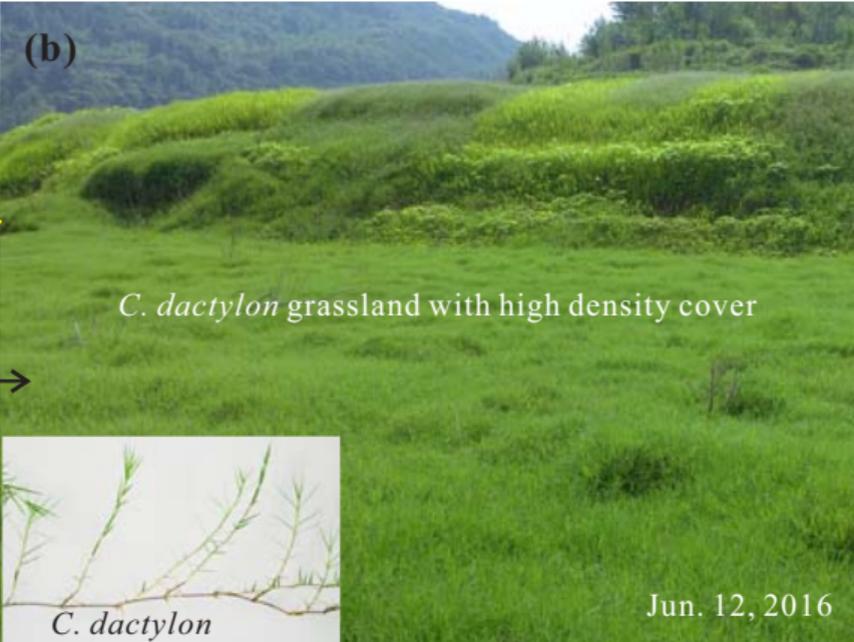
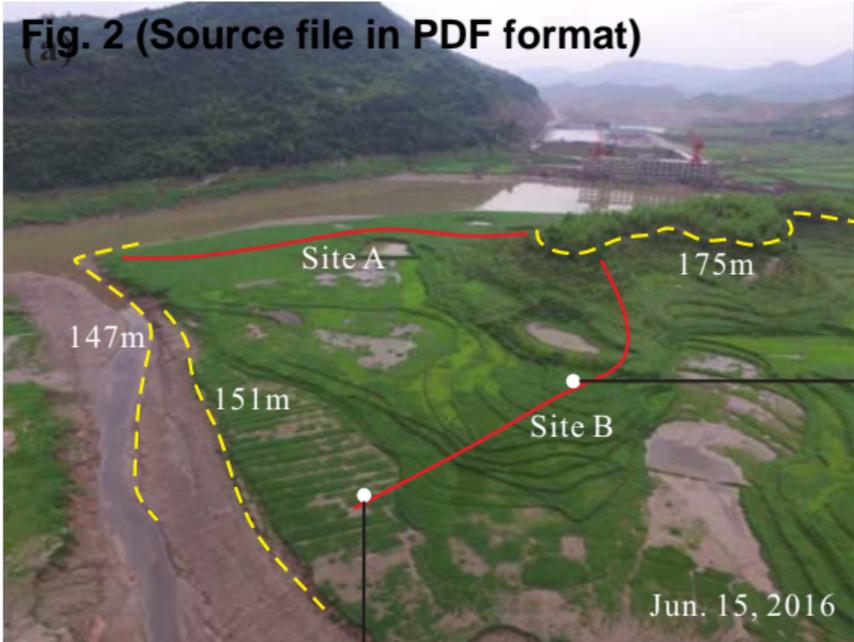


Fig. 2 (Source file in PDF format)



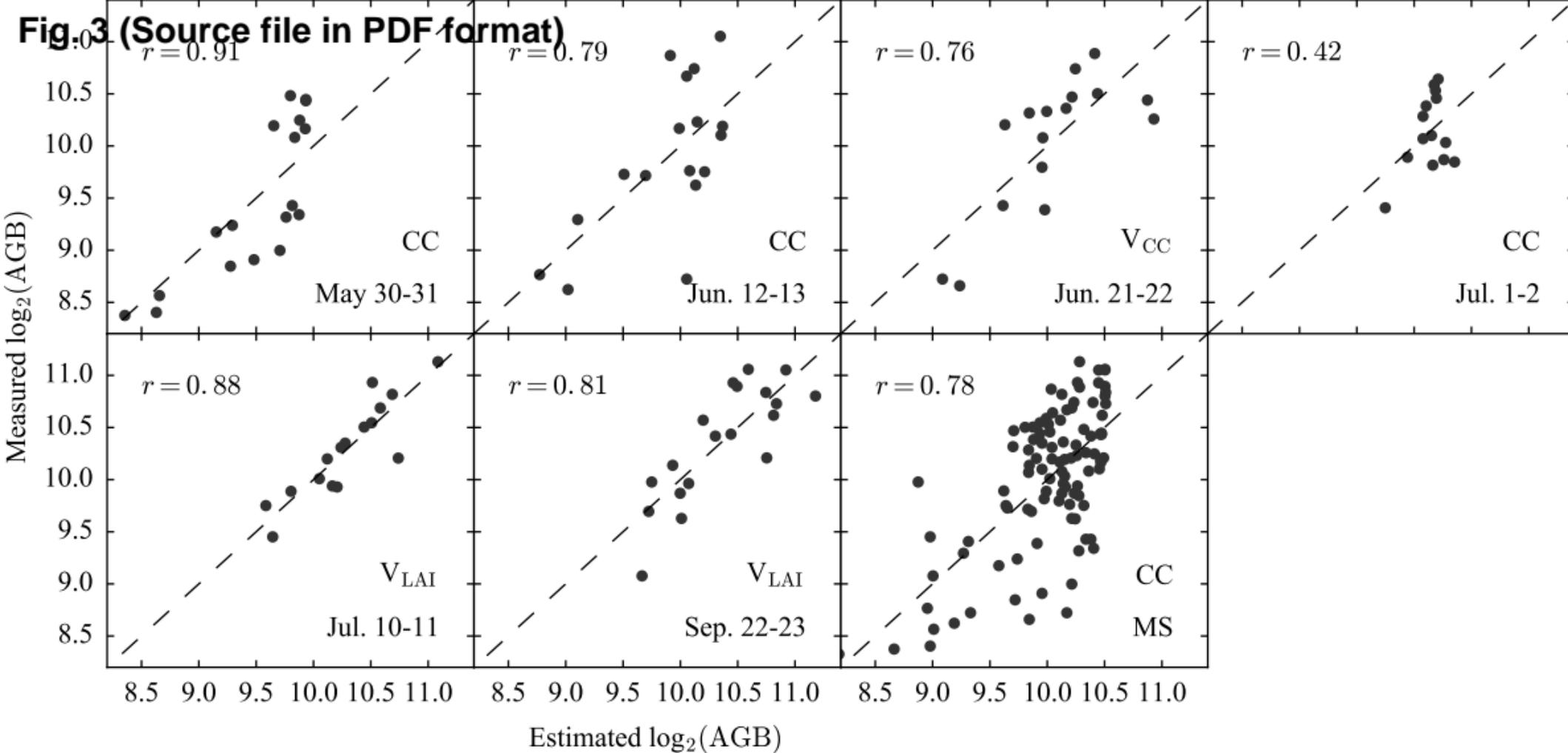


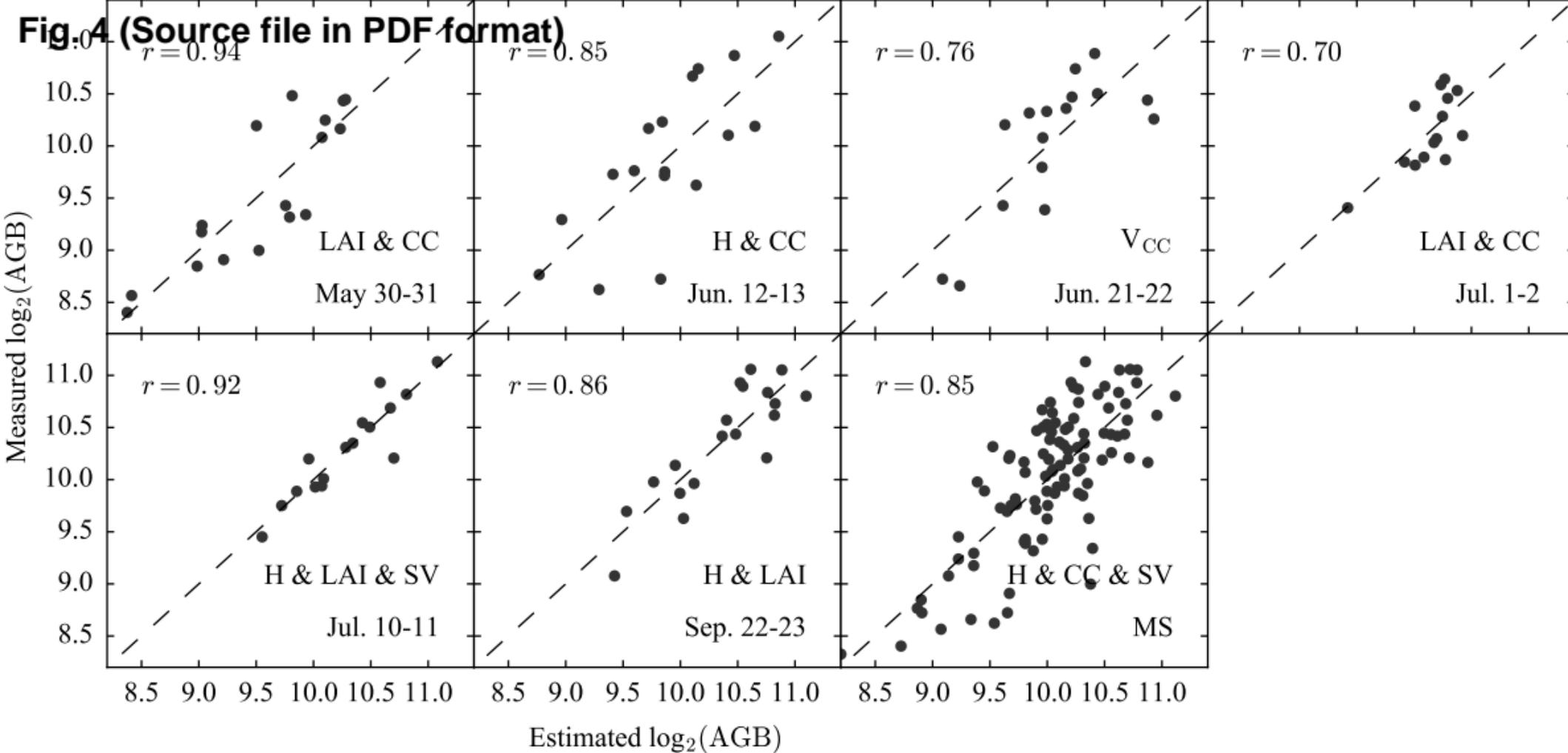
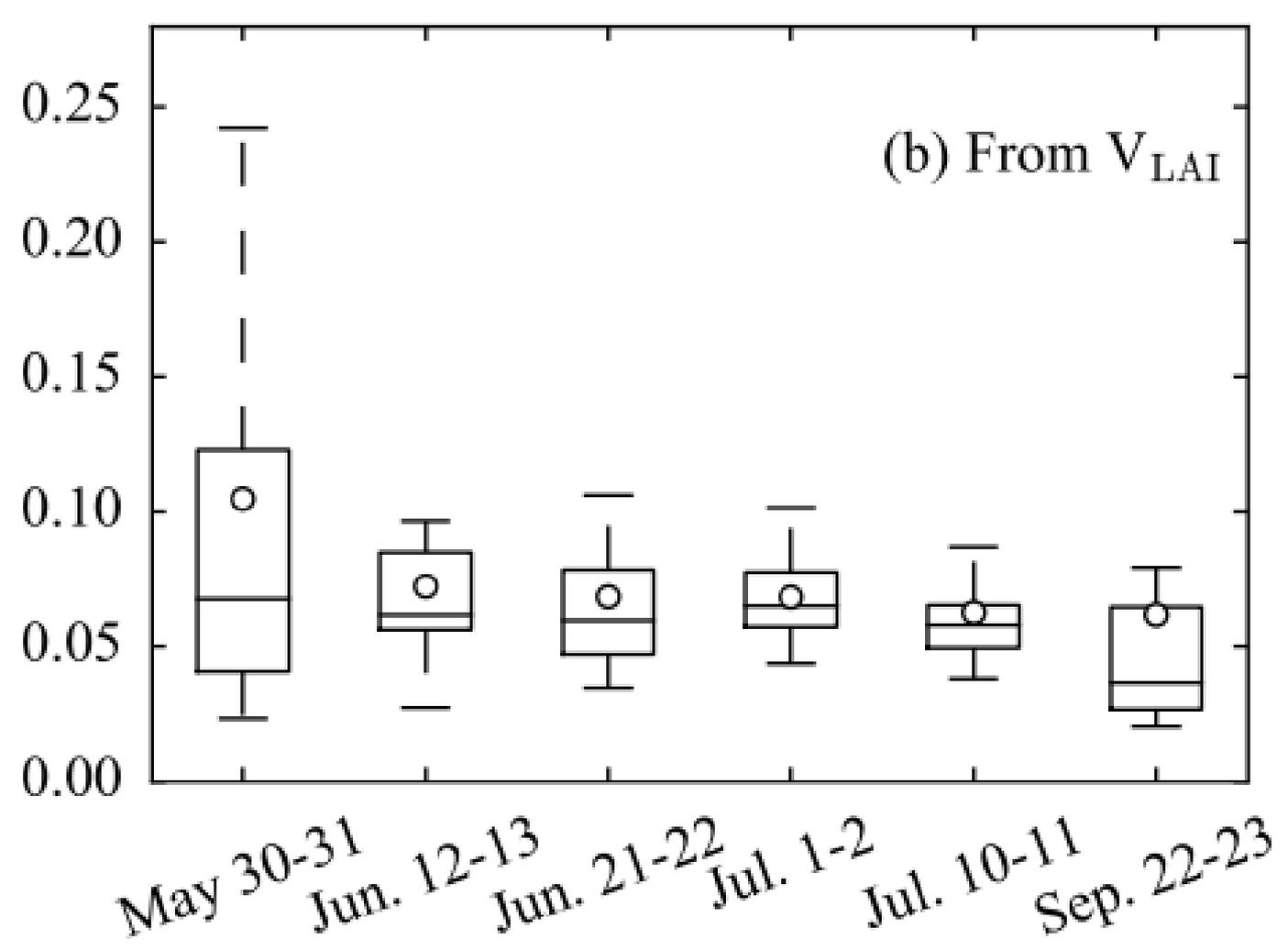
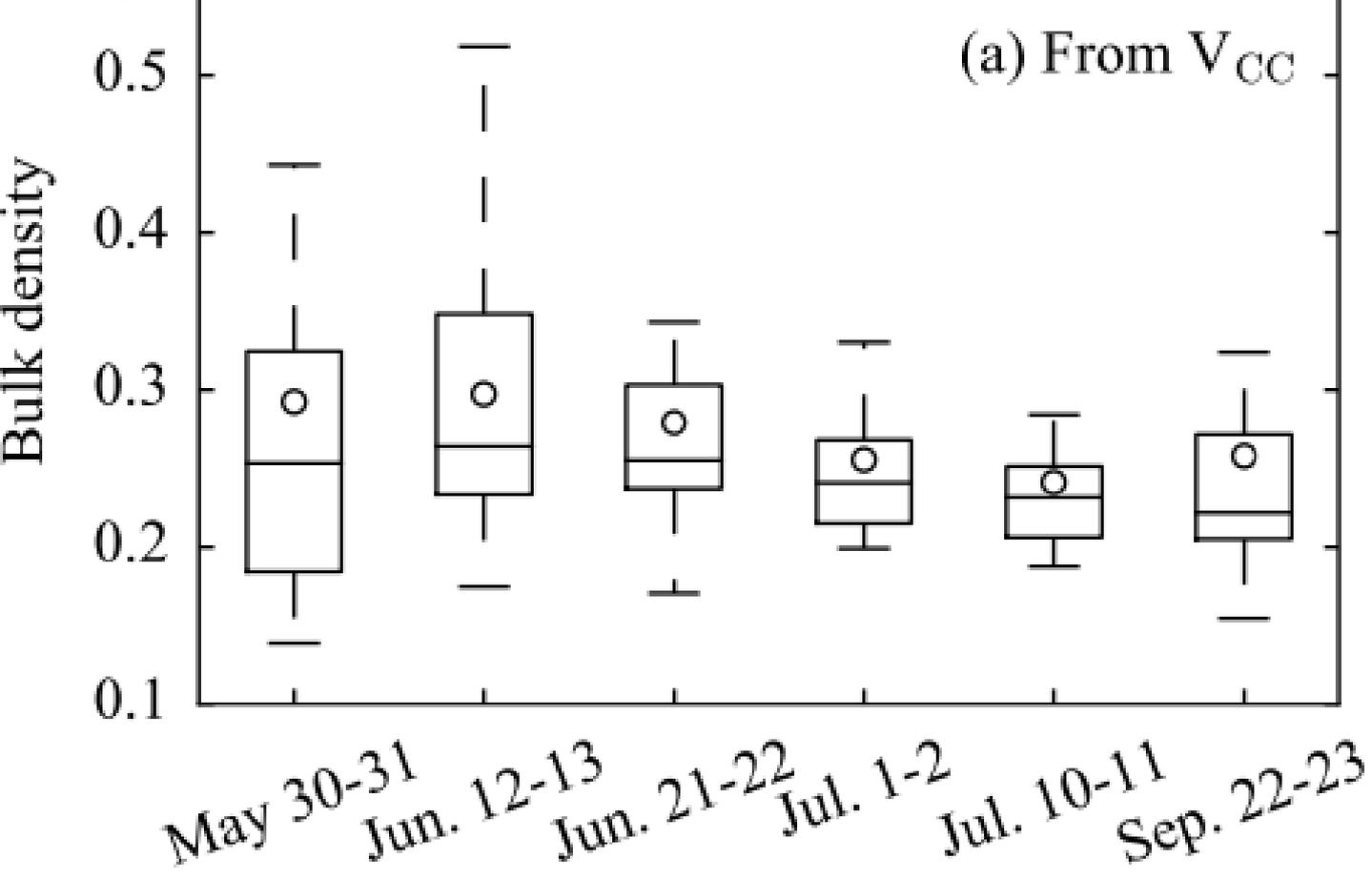
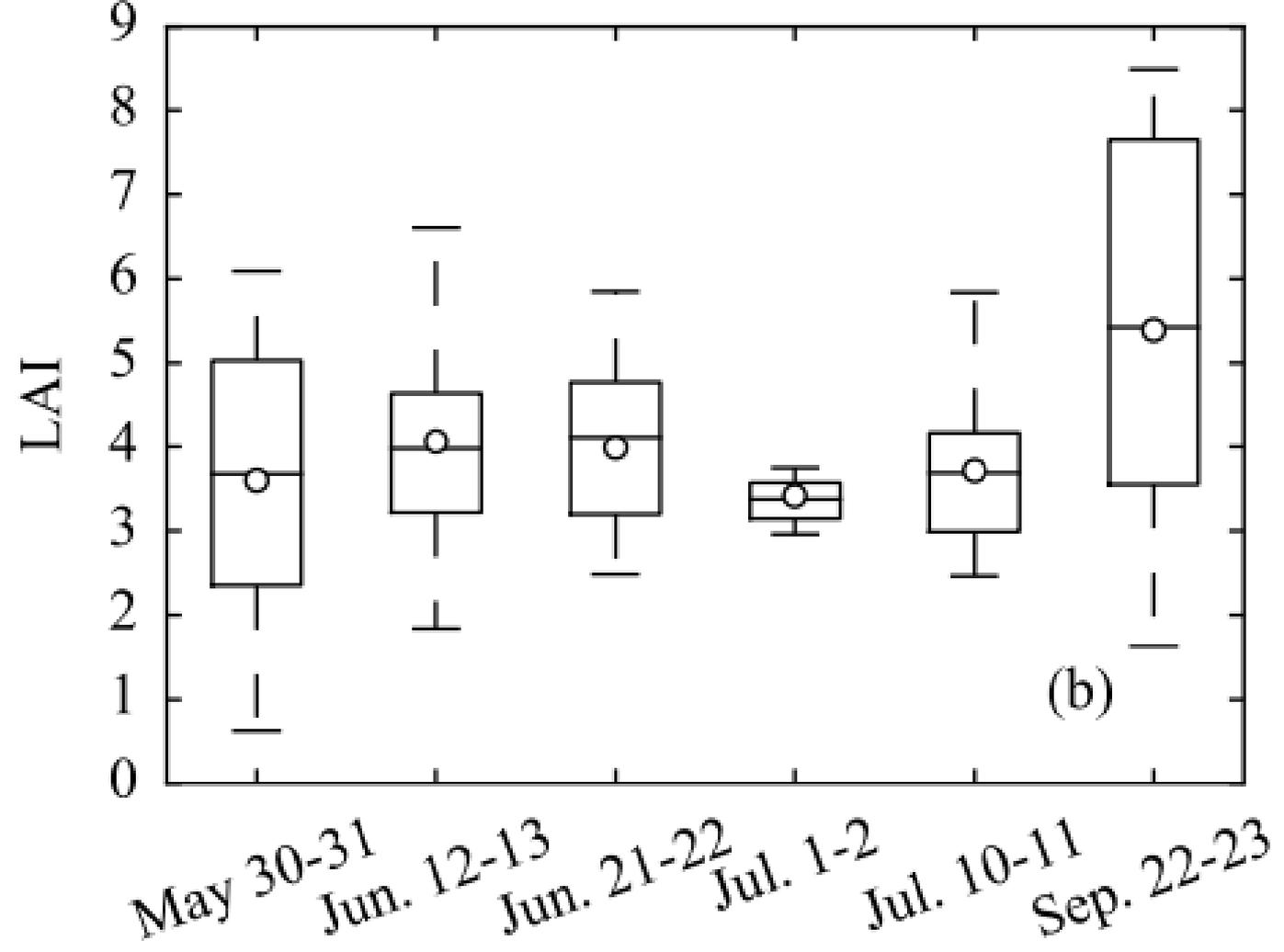
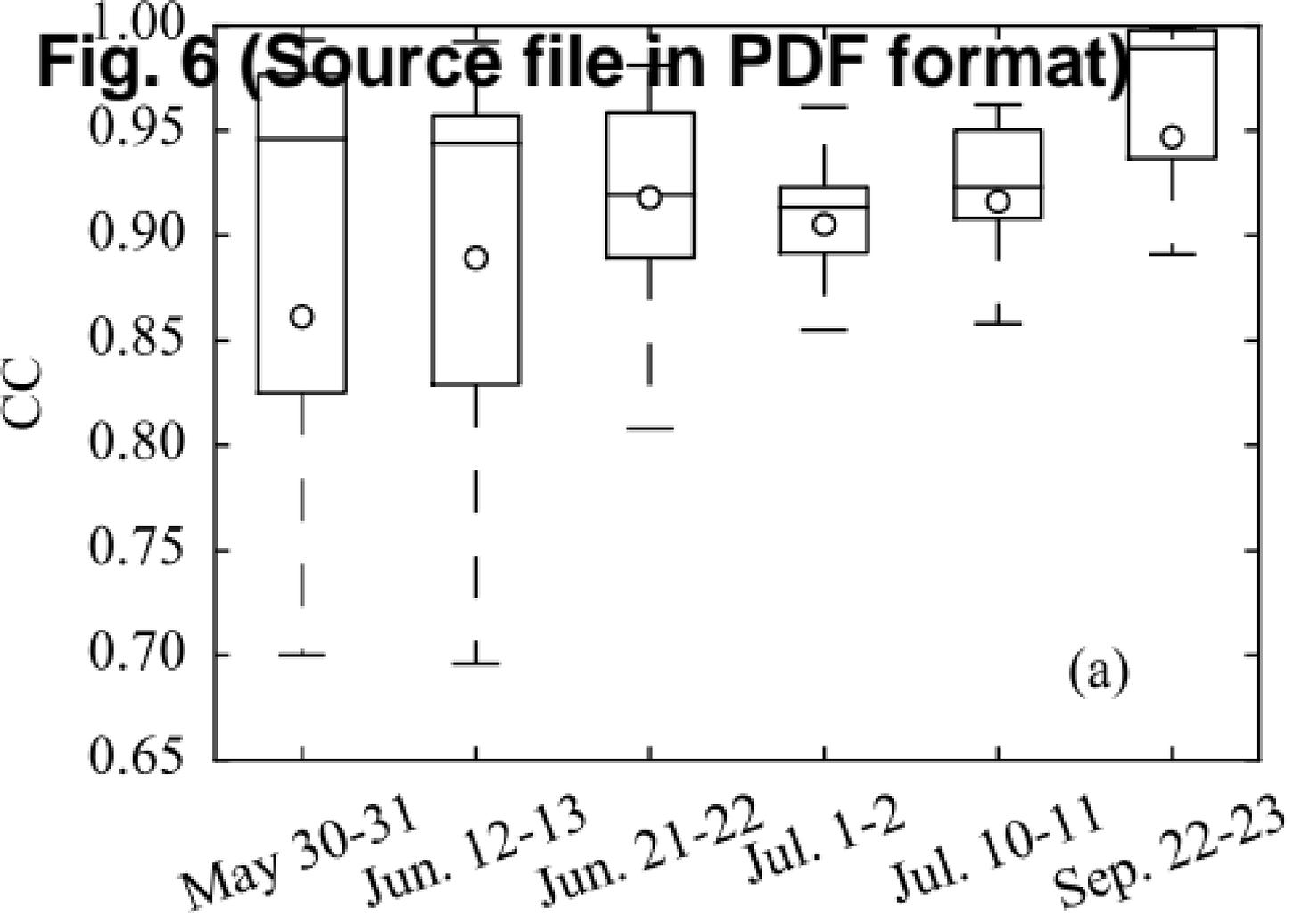
Fig. 4 (Source file in PDF format)

Fig. 5 (Source file in PDF format)





Interactive Map file (.kml or .kmz)

[Click here to download Interactive Map file \(.kml or .kmz\): Sampling sites.kmz](#)