How much biomass do plant communities pack per unit volume?

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Aboveground production in terrestrial plant communities is commonly expressed in amount of carbon, or biomass, per unit surface. Alternatively, expressing production per unit volume allows the comparison of communities by their fundamental capacities in packing carbon. In this work we reanalyzed published data from more than 900 plant communities across nine ecosystems to show that standing dry biomass per unit volume (biomass packing) consistently averages around 1 kg/m^3 and rarely exceeds 5 kg/m^3 across ecosystem types. Furthermore, we examined how empirical relationships between aboveground production and plant species richness are modified when standing biomass is expressed per unit volume rather than surface. We propose that biomass packing emphasizes species coexistence mechanisms and may be an indicator of resource use efficiency in plant communities.

2   **How much biomass do plant communities pack per unit volume?**

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15   *Short title*: Biomass packing in plant communities

16   **Abstract**

17   Aboveground production in terrestrial plant communities is commonly expressed in amount of carbon,

18   or biomass, per unit surface. Alternatively, expressing production per unit volume allows the

19   comparison of communities by their fundamental capacities in packing carbon. In this work we

20   reanalyzed published data from more than 900 plant communities across nine ecosystems to show that

21   standing dry biomass per unit volume (biomass packing) consistently averages around 1 kg/m^3 and

22   rarely exceeds 5 kg/m^3 across ecosystem types. Furthermore, we examined how empirical relationships

23   between aboveground production and plant species richness are modified when standing biomass is

24   expressed per unit volume rather than surface. We propose that biomass packing emphasizes species

25   coexistence mechanisms and may be an indicator of resource use efficiency in plant communities.

26

27   **Introduction**

28   Uncovering general principles that govern the functioning of ecosystems is a long standing objective of

29   community ecology. One such principle, the self-thinning rule, predicts that the standing biomass of

30   plant communities increases with decreasing stem density in crowded stands (Hutchings, 1979,

31   Westoby, 1984). D.E. Weller (1989) proposed a simple geometric model of the self-thinning rule in

32   which the standing biomass (g/m^2) of different communities is negatively correlated to stem density.

33   When expressed per unit volume (g/m^3) however, his model also predicted that standing biomass

34   should be independent of stem density across the plant kingdom (Weller, 1989).

35   Absence of a general relationship between standing biomass per unit volume and stem density across a

36   range of ecosystems would have two important implications. First, it would evince that plants cannot

37   allocate more carbon to aboveground compartments than imposed by competition for volumetric

38   resources, such as light. Secondly, plant communities would differ from one another in their capacity

39   to grow tall, yet compare in their capacity to pack carbon. Weller (1989) reported a positive

40   relationship between dry biomass per unit volume and stem density, suggesting more efficient carbon

41   packing in communities growing at a higher density. However, Weller's relationship relied on two

42   datasets and, thus, remains inadequately tested.

43   Aboveground production, or yield, in terrestrial plant communities is commonly measured in amount

44   of dry biomass per unit surface. Alternatively, expressing production per unit volume could better

45   reflect how plants utilize all dimensions of the space in which they grow, hence emphasizing

46   coexistence mechanisms. For instance, plants adapted to grow in the shade may contribute to biomass

47   packing by filling the understorey space more efficiently (Claveau, Messier & Comeau, 2005,

48   Valladares & Niinemets, 2008). Moreover, plants characterized by different growth rates or lifespans

49   may increase biomass packing by acquiring resources on different spatial or time scales (Augspurger,

50   2008).

51   Biomass packing can be conceptualized as the amount of standing vegetation living within a sampling

52   box. This box delineates a three-dimensional space, either physical or virtual, within which the

53   vegetation is confined. Thus, biomass packing represents the amount of standing vegetation (expressed

54   as dry biomass or occupied plant volume) scaled per unit of sampled volume.

55   The present study addresses two questions: Are there fundamental limits to the amount of standing dry

56   biomass that is packed per unit volume in terrestrial plant communities? Is biomass packing affected by

57   community composition and species richness? To investigate these questions we reviewed the

58   scientific literature and compiled data for more than 900 plant communities. This synthesis highlights

59   broad patterns in biomass packing across contrasted ecosystem types. It is not a meta-analysis of the

60   reviewed literature, which would require the inclusion of climatic or edaphic moderator variables as

61   well as accounting for spatial auto-correlation and random (data source) effects.

62

63   **Materials & Methods**

64   We searched the scientific literature for studies reporting both dry standing biomass per unit surface

65   and mean height of canopy plants in vegetation stands. The search targeted studies that monitored

66   vegetation stands close to their peak of biomass production (Table 1). We converted all biomass values

67   to g/m^2 and height values to m (Table S1). In the literature, we found only Weller's study (1989)

68   reported direct measures of biomass per unit volume in terrestrial ecosystems. As such, Weller's

69   dataset was not used in our analysis, but as a benchmark to compare those results against. From all

70   other aggregated data, we calculated the packing density of each plant community by dividing standing

71   dry biomass per unit surface by community height.

72   In addition to biomass and height, three of the data sources also included the species richness of their

73   respective plant community (Table S1): meadow, wetland and grassland. This data subset of 533

74   communities allowed us to examine how expressing standing biomass per unit surface or unit volume

75   modifies the relationship between biomass production and plant species richness.

76   To determine whether standing dry biomass approximates the volume occupied by plants, we compiled

77   a dataset on 42 wetland plant communities from the Lac St-Pierre ecosystem (Québec, Canada). In

78   August 2014, we sampled vegetation quadrats of 0.5 x 0.5m covering a broad range of species

79   assemblages and vegetation types. In each quadrat we clipped all the vegetation standing above 2cm

80   from the ground. We then evaluated plant volume using the water displacement method in a bucket of

81   12.6 cm radius. We expressed the amount of water displaced by the submersed vegetation in cubic

82   meters. We then oven dried the vegetation at 70°C for 48h and weighed the dry biomass. Finally, we

83   report the relationship between plant volume (m^3/m^2) and standing dry biomass (g/m^2) to evaluate their

84   association.

85

86   **Results**

87   From our analysis of the reviewed data we found that standing dry biomass per unit surface varied by

88   over three orders of magnitude across the plant kingdom (Fig. 1). In forest ecosystems, dry biomass per

89   unit surface typically ranged between 10 and 100 kg/m^2, with pacific and tropical forest communities

90   consistently reaching higher values than that of temperate and boreal forests. In contrast, the standing

91   biomass of croplands and grasslands was comparable to one another, falling just above 1 kg/m^2 on

92   average. Lastly, meadows cumulated around 0.3 kg/m^2 standing dry biomass, though biomass increased

93   with increasing species richness, up to 0.5 kg/m^2 in the 60-species communities (slope = 0.0037, R^2 =

94   0.06, df = 338, t = 4.5, p < 0.001).

95   When expressing the standing dry biomass of the 971 communities in our dataset per unit volume,

96   biomass packing varied around 1 kg/m^3 (the average 50th percentile being 0.88 kg/m^3) and by less than

97   an order of magnitude across ecosystems (Fig. 1). The 75th percentile for biomass packing across

98   ecosystems ranged from 0.81 kg/m^3 in croplands up to 1.82 kg/m^3 in pacific forests, suggesting high

99   overall consistency relative to measures of biomass per unit surface (Fig. 1). Biomass packing reached

100 an overall maximum at 4.7 kg/m^3 in one pacific forest plot.

101 The positive relationship between plant species richness and biomass production among experimental

102 meadow communities vanished when standing dry biomass was expressed per unit volume rather than

103 surface (slope = 0.0004, R^2 < 0.01, df = 338, t = 0.3, p = 0.738, Fig. 1). In other herbaceous ecosystems

104   (Fig. 2), the relationship between plant species richness and biomass production shifted from negative,

105   when biomass was expressed per unit surface (slope = -0.063, R^2 = 0.12, df = 191, t = -5.2, p < 0.001),

106   to nonexistent when expressed per unit volume (slope = 0.018, R^2 < 0.01, df = 191, t = 1.3, p = 0.180).

107   We compared two methods of quantifying the amount of standing vegetation for wetland plant

108   communities. The relationship between dry biomass and plant volume was strong and linear (Pearson's

109   r = 0.86), indicating that standing biomass is a good proxy for the volume occupied by plant modules,

110   at least for wetland communities (Fig. 3).

111

112   **Discussion**

113   *Fundamental limits to biomass packing*

114   The literature review highlights that if plant community biomass is represented as dry biomass per unit

115   surface area, major ecosystem types are drastically different. However, when accounting for height and

116   expressing standing dry biomass per unit volume, plant communities from different ecosystems appear

117   remarkably similar in their capacity to pack biomass. Biomass packing across plant communities

118   peaked just below 5 kg/m^3, with an average median across ecosystems close to 1 kg/m^3. These values

119   are strikingly similar to those originally reported by Weller (1989) for mono-specific stands; reporting

120   a maximum value of 5.2 kg/m^3 (median of 1.2 kg/m^3) in the first dataset and 5.3 kg/m^3 (median of 0.6

121   kg/m^3) in the second. We feel confident that the inclusion of more plant communities would not alter

122   these general results.

123   Our results revealed that cropland and meadow communities were equally capable of packing biomass

124   per unit volume. However, the caveat to this result is that it is true only when plant communities are

125   compared at their peak of biomass production. For instance, cornfields sown in widely spaced rows

126   attain their maximum of biomass packing only towards the end of the growing season. Likewise,

127   meadows are repeatedly harvested within a year, after which a regrowth period of sparse vegetation

128   and low biomass packing initiates. Moreover, while tropical and temperate forests may show similar

129   packing values at their peak of production, air temperature and sunlight duration impose stronger

130   seasonal variations in the biomass packing of temperate ecosystems. Such examples illustrate the

131   importance of accounting for changes in biomass packing over time and, perhaps, the inaccuracy of

132   treating it as a static metric.

133   Perhaps the most contentious issue when assessing biomass packing is how the vertical dimension of

134   the sampling box is measured. Here, the upper boundary of that box was defined as the mean height of

135   canopy plants. In our review, one case study did use a physical, rather than a virtual, sampling box to

136   assess the biomass packing of young (< 18 years old) forest stands (Peterson et al., 1982). In this study,

137   sampling boxes of $1m^3$ were placed in 107 woody stands, such that stems would fill the frames from

138   top to bottom. Overall, the maximum biomass packing measured across stands and vegetation types

139   varied from 3 kg/m^3 in poplar and birch forests to 6 kg/m^3 in pine and spruce forests (Peterson et al.,

140   1982). Since sampling frames in this study were systematically placed in the densest portions of the

141   forest, the above values represent upper bounds of dry biomass per unit volume. Hence, although

142   measures of community height among studies might differ slightly, the biomass packing limit of ca. 5

143   Kg/m^3 that we identified is in fair agreement with the upper bounds independently reported by Peterson

144   et al. (1982) and Weller (1989).

145   *Species richness and biomass packing*

146   Garnering much attention in the literature, positive relationships between species richness and biomass

147   production have been repeatedly reported in experimentally manipulated plant communities (e.g.,

148   Reich et al. 2012). Further analyses of such experiments have determined that the relationship arises

149   from a more efficient use of resources in species-rich communities over that of species-poor ones, or

150   the so-called complementarity effect (Cardinale et al. 2007, Reich et al. 2012). Plant communities in

151   the Jena Biodiversity Experiment, also used here as a data source, are no exception to this trend

152   (Marquard et al. 2009). In contrast to the positive relationship between species richness and biomass

153   per unit surface, our results show that species-rich meadows in the Jena Experiment do not pack more

154   biomass per unit volume; that is, the richness-packing relationship is flat.

155   Divergent from those aforementioned biodiversity experiments, a negative relationship between plant

156   species richness and biomass production can be observed in freely assembled herbaceous communities,

157   wherein the productive stands are dominated by fewer species (Waide et al. 1999). The negative tail of

158   the richness-production relationship has been explicated by facilitation and competitive exclusion

159   processes among plant species growing in the most fertile situations (e.g., Michalet et al. 2006). In the

160   present study, we did observe a higher biomass per unit surface in species-poor herbaceous

161   communities, and therefore a negative richness-production relationship, but again the relationship

162   vanished when standing dry biomass was expressed per unit volume. Stated simply, plant species

163   richness had no effect on the biomass packing of plant communities at their peak of production.

164   To understand why the richness-biomass relationship flattens when expressing biomass per unit

165   volume, we examined how much of the variation in standing biomass per unit surface is explained by

166   community height. Among our 971 plant communities, height explains 88% of the variation in

167   standing biomass when the axes are on a logarithmic scale (Table S1). This strong correlation suggests

168   that, both, community height and biomass per unit surface are likely driven by similar factors affecting

169   resource use and availability (Moles et al. 2009). Dividing standing dry biomass by community height

170   would emphasize the local species coexistence processes that are independent of stand fertility and

171   climate conditions, but the assertion remains to be fully tested.

172

173   **Conclusions**

174   Our reanalysis of the literature casts a new light on how plant biomass accumulates in terrestrial

175   ecosystems. Specifically, while the widespread metric of biomass per unit surface highlights

176   differences between plant communities, expressing their standing dry biomass per unit of volume

177   reveals their striking similarity. Expressing biomasses per unit volume goes against a longstanding

178   tradition of measuring primary production per unit surface in terrestrial ecosystems, probably reflecting

179   our utilitarian view of ecosystems conditioned by questions such as: how much crop (e.g., wood, hay,

180   or grain) can be produced and harvested per hectare of land?

181   Our findings suggest that biomass packing is influenced less by baseline climatic and edaphic

182   conditions, but rather emphasizes local plant-plant interactions. We propose that a fundamental limit

183   might exist to the amount of dry biomass that natural plant communities pack per unit volume in

184   terrestrial ecosystems; since the long-term maintenance of standing dry biomass beyond this point may

185   be biologically unsustainable (Hutchings 1979). It is likely that this approximate limit of 5 kg/m^3 can

186   be exceeded in communities grown under controlled conditions, although croplands did not reach

187   higher biomass packing values over that of other ecosystems in our dataset. Biomass packing may thus

188   represent a simple and generic indicator of resource use efficiency in plant communities.

189

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246   **Figure captions**

247

248   **Fig. 1.** Standing dry biomass of plant communities in different ecosystems when biomass is expressed

249   (a) per unit surface or (b) per unit volume.

250   **Fig. 2.** Relationship between species richness and dry standing biomass of plant communities in two

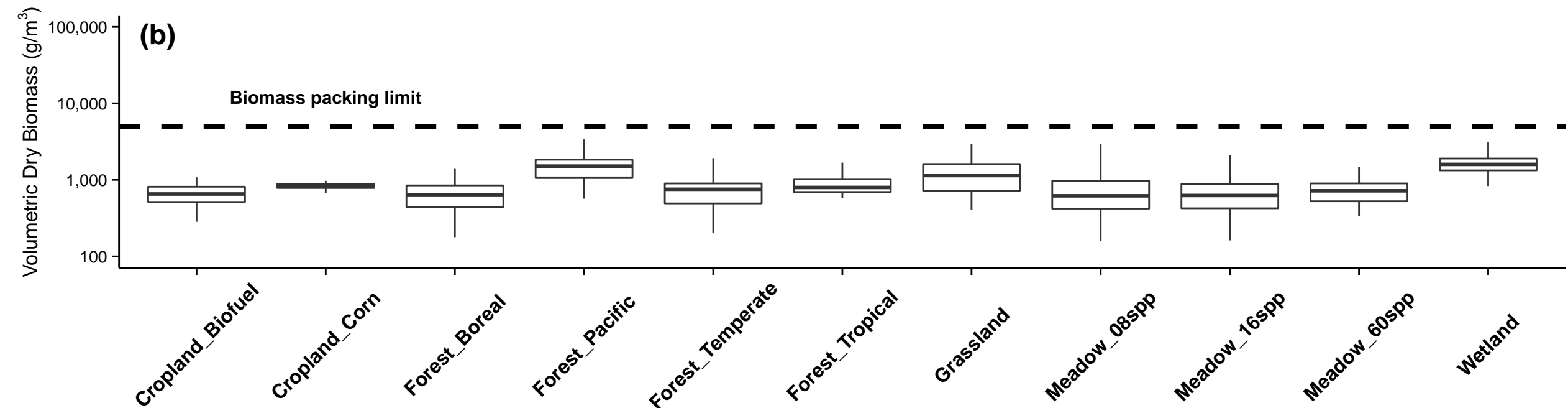
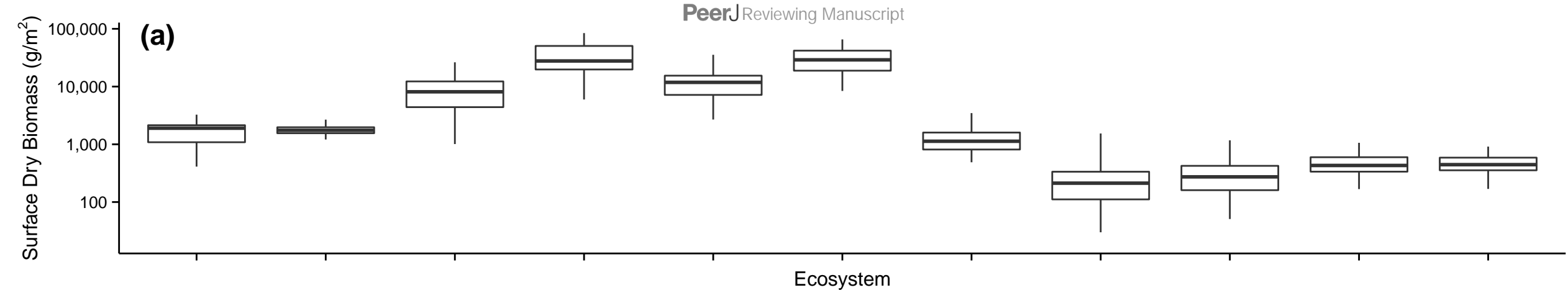
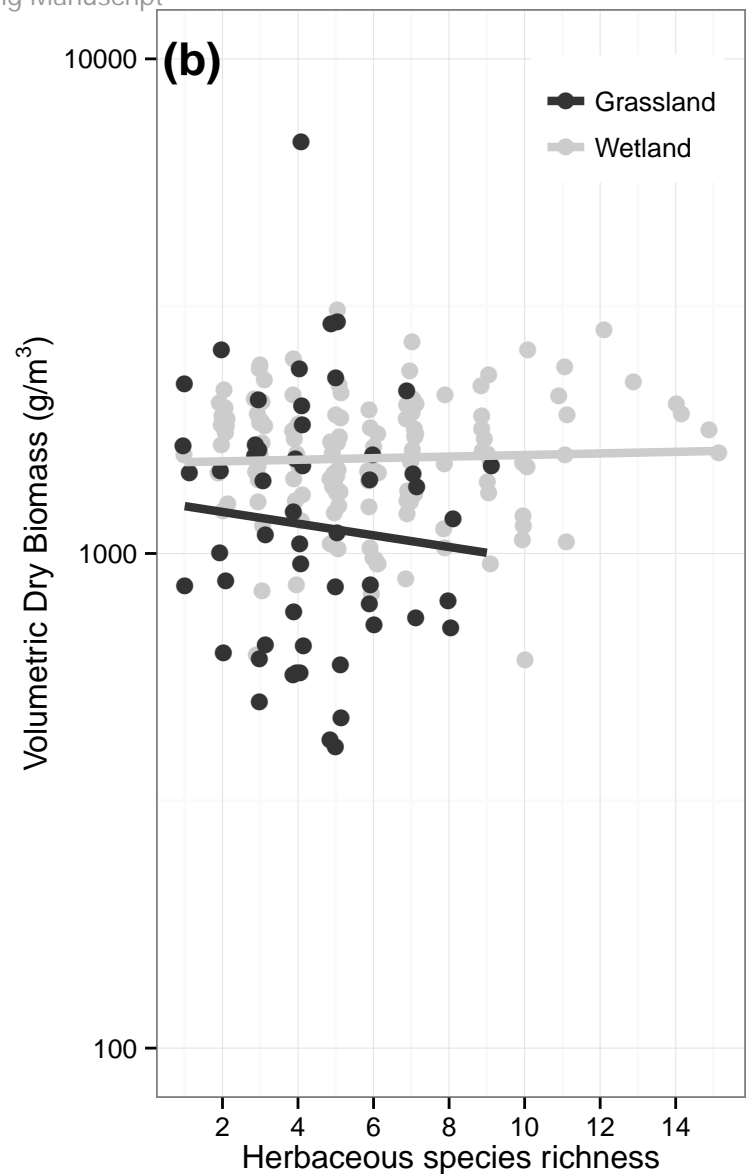
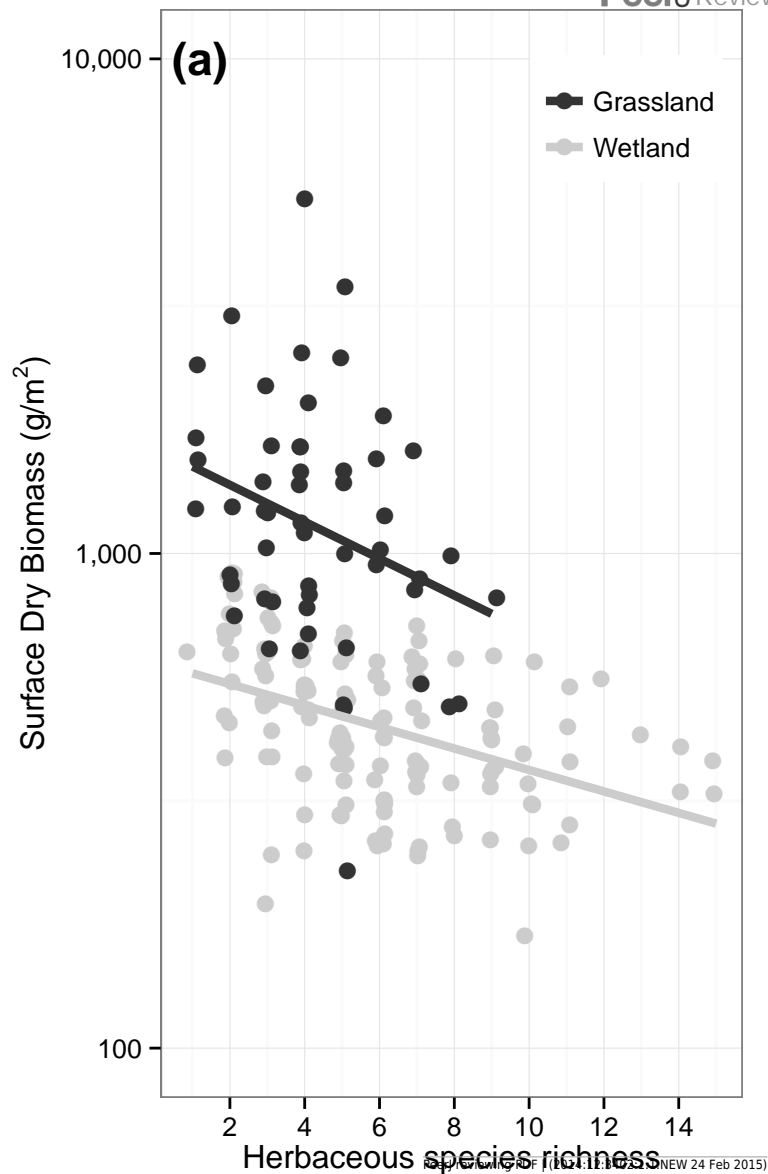
251   herbaceous ecosystems when biomass is expressed (a) per unit surface or (b) per unit volume.

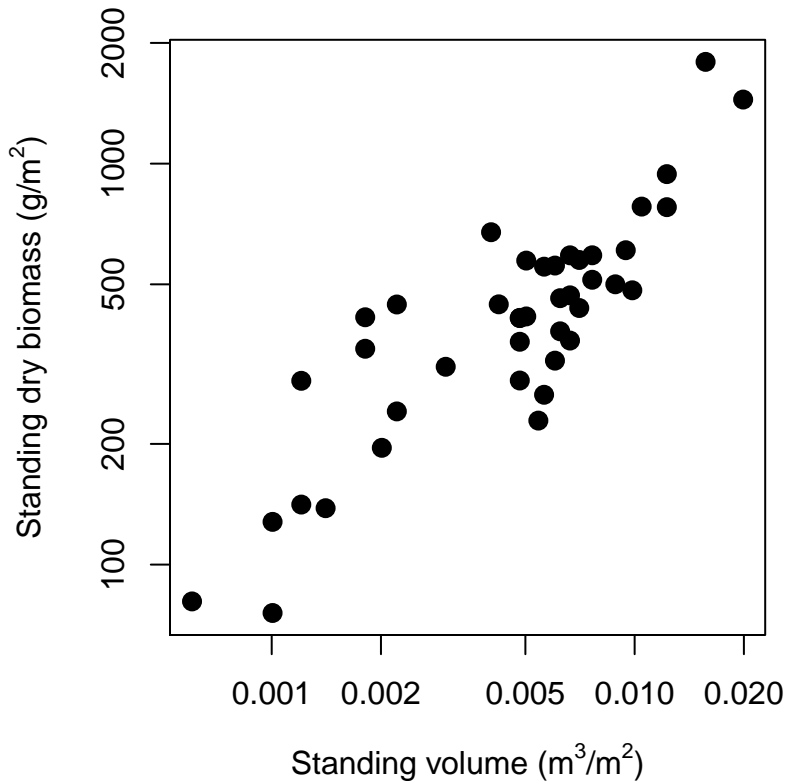
252   **Fig. 3.** Comparison of two methods of assessing the amount of standing vegetation in wetlands of the

253   Lac St-Pierre (Québec, Canada). The aboveground production of 42 plant communities is expressed in

254   units of dry biomass (g/m^2) or of occupied plant volume (m^3/m^2)

255

Standing dry biomass of plant communities in different ecosystems when biomass is expressed (a) per unit surface or (b) per unit volume.

Relationship between species richness and dry standing biomass of plant communities in two herbaceous ecosystems when biomass is expressed (a) per unit surface or (b) per unit volume.

Comparison of two methods of assessing the amount of standing vegetation in wetlands of the Lac St-Pierre (Québec, Canada).

The aboveground production of 42 plant communities is expressed in units of dry biomass (g/m^2) or of occupied plant volume (m^3/m^2).

Ecosystems and plant communities (No. stands) from various sources reporting both total dry standing biomass per unit surface and mean height of canopy plants.

Ecosystem	No. stands	Location	Sources
Croplands - Biofuel	19	USA	(Propheter et al. 2010)
Cropland - Corn	13	USA	(Wilhelm et al. 2011)
Forest - Tropical	19	Columbia, Cambodia, Thailand, Venezuela, Malaysia, Borneo, Puerto Rico	(Yamakura et al. 1986, Weaver and Murphy 1990)
Forest – Pacific (west-coast)	45	Canada	(Gillis et al. 2005)
Forest - Temperate	174	USA, Canada	(Whittaker et al. 1974, Gillis et al. 2005)
Forest - Boreal	126	Canada	(Gillis et al. 2005)
Grasslands	53	Canada	(Rheault et al. 2014)
Meadows – 8, 16 & 60 species	340	Germany	(Weigelt et al. 2010)
Wetlands	182	France, Canada	(Violle et al. 2011, Proulx et al., unpublished †)

2   † Data are presented in Appendix 1