Aboveground biomass increments over 26 years (1993–2019) in an old-growth cool-temperate forest in northern Japan

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Abstract

Assessing long-term changes in biomass of old-growth forests is critical in evaluating forest ecosystem functions under a changing climate. Long-term biomass changes are the result of accumulated short-term changes, which can be affected by endogenous processes such as gap filling in small-scale canopy openings. Here, we used 26 years (1993–2019) of repeated tree census data in an old-growth, cool-temperate, deciduous mixed forest that contains three topographic units (riparian, denuded slope, and terrace) in northern Japan to document decadal changes in aboveground biomass (AGB) and their processes in relation to endogenous processes and climatic factors. AGB increased steadily over the 26 years in all topographic units, but different tree species contributed to the increase among the topographic units. AGB gain within each topographic unit exceeded AGB loss via tree mortality in most of the measurement periods despite substantial temporal variation in AGB loss. At the local scale, variations in AGB gain were partially explained by compensating growth of trees around canopy gaps. Climate affected the local-scale AGB gain: the gain was larger in the measurement periods with higher mean temperature during the current summer but smaller in those with higher mean temperature during the previous autumn, synchronously in all topographic units. The decadal climate trends of warming are likely to have contributed to the steady increase in AGB in this old-growth forest.

35   Key words: forest biomass · long-term data · Kanumazawa Riparian Research Forest ·

36   temperature

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Introduction

39   Old-growth forests are widely recognized to play an important role in the carbon cycle

40   (Luyssaert et al. 2008). It has been commonly accepted that old-growth forests are carbon

41   neutral (Odum 1969) and their aboveground biomass (AGB) is at 'steady state', with equal

42   gross primary production and respiration (Bormann and Likens 1979). However, recent

43   studies indicate that they grow continuously (Foster et al. 2014) and work as carbon sinks

44   with increasing biomass over centuries (Luyssaert et al. 2008). As biomass growth of old-

45   growth forests is more susceptible to climate change than that in young forests (Chen et al.

46   2016), assessing long-term changes in biomass of old-growth forests is critical in evaluating

47   the effects of climate change on forest ecosystem functions (McDowell et al. 2020).

48   Long-term changes in biomass result from the accumulation of short-term changes in the

49   form of gain due to tree growth and loss due to mortality (Hoshizaki et al. 2004). Therefore,

50   to understand how climate affects changes in AGB, the effects of climatic factors on each

51   component need to be taken into account (Chen and Luo 2015; Peña et al. 2018). In addition,

52   endogenous processes such as gap filling in small-scale canopy openings can drive biomass

53   change (Phillips et al. 2009; McDowell et al. 2020): at the local scale, gap formation may

54   cause first a decrease and then an increase in AGB caused by growth promotion of trees

55   around the gap. Repeatedly measured tree census data with tree location can be useful in

56   revealing these processes.

57   Environmental factors such as topographic position affect both forest biomass (Kubota et

58   al. 2004; Valencia et al. 2009) and tree species composition (Chen and Luo 2015;

59   Kuuluvainen et al. 2017; Ohmann and Spies 1998). For instance, on northern Honshu, Japan,

60   *Fagus crenata* often dominates forest stands on hillslopes, whereas more tree species occur in

61   riparian areas (Suzuki et al. 2002). Tree species in riparian forests have diverse life history

62   traits (e.g., both shorter and longer lifespans, heavy sprouting; Nakamura and Inahara 2007;

63   Sakio 2020). Therefore, hillslope and riparian stands are expected to differ in the dynamics

64   (i.e., growth and mortality) and, consequently, the pattern of biomass changes in component

65   species. In addition, a recent analysis of long-term tree census data in northern Japan has

66   revealed different responses among species to changing climate and consequent changes in

67 stand structure and species composition (Hiura et al. 2019). Thus, stands with different

68 topographic characteristics can show different responses to climate change.

69   Here, we quantify decadal changes in AGB and their processes in relation to endogenous

70 processes and climatic factors, using tree census data measured repeatedly over 26 years

71 (1993–2019) in an old-growth, cool-temperate deciduous mixed forest with different types of

72 topographic units in northern Japan. We ask the following questions: (1) Did AGB show net

73 increase or decrease over the whole forest and study period? (2) Did tree species contribute

74 differently to biomass change among the different types of topographic units? (3) How did

75 gain and loss contribute to the overall changes in stand biomass? (4) Did climatic factors and

76 endogenous processes such as canopy gap formation and recovery influence short-term

77 changes in AGB at the local scale?

Materials and methods

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Study site

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80 The study was conducted in the Kanumazawa Riparian Research Forest (KRRF) in Iwate,

81 northern Japan (39°06′N, 140°51′E), an old-growth forest with no record of significant

82 anthropogenic disturbances. In KRRF, tree community dynamics have been repeatedly

83 measured since the establishment of a 4.71-ha permanent plot in 1993 (Fig. 1; Suzuki et al.

84 2002). This site is one of the core research sites of the Japan Long-Term Ecological Research

85 Network (JaLTER). KRRF has a cool-temperate climate with a mean annual temperature of

86 8.8 °C and a warmth index (Kira 1991) of 71 °C month (Noguchi et al. unpublished). The

87 mean annual precipitation is 2000 mm, and snow cover lasts 5 months with maximum snow

88 depth of approximately 2 m (Oki et al. 2013). The vegetation depends on the topographic unit.

89 The riparian area is covered with a species-rich deciduous broadleaved forest consisting of

90 both riparian specialists (*Cercidiphyllum japonicum*, *Aesculus turbinata*, *Acer mono*,

91 *Pterocarya rhoifolia*, and *Ulmus laciniata*) and habitat generalists (*Fagus crenata* and

92 *Quercus crispula*) (Masaki et al. 2008; Suzuki et al. 2002). The upper slopes and terrace are

93 dominated by *F. crenata* and *Q. crispula*. Detailed information on the ecology of component

94 species is available in Hoshizaki et al. (1997, 1999), Masaki et al. (2005), and Osumi (2006).

95 The age of the largest *C. japonicum* individual is estimated to be more than 500 years (Osumi

96 2006), indicating that this forest is sufficiently old-growth. The natural disturbance regime in

97 KRRF is characterized by canopy gap formation and fluvial sediment movements (Oki et al.

98 2013). Gap-creating disturbance occurs about every 1 to 3 years, with gap size ranging from

99   tens to hundreds of square meters (Oki et al. 2013). Recent fluvial sediment movements were

100 recorded in 1988, 1998, and 2007, causing ground disturbance with sizes ranging from 144

101 m^2 to 680 m^2 but no damage to canopy trees.

102 **Field measurement**

103 The 4.71-ha permanent plot was divided to 471 10-m × 10-m quadrats (Fig. 1). The plot

104 ranges in elevation from 400 to 460 m a.s.l., and includes three topographic units: riparian

105 (3.11 ha), terrace (1.06 ha), and denuded slope between them (0.57 ha). In the whole plot, all

106 stems greater than 5 cm in diameter at breast height (DBH) were tagged for identification and

107 mapped, and DBH was measured at the same marked location on each stem every 2 years

108 from 1993 to 1999 and every 4 years from then to 2019.

109 **Estimation of AGB change and its components**

110 We calculated tree AGB, basal area (BA), and stem density in each topographic unit.

111 Individual tree AGB was estimated by using a general allometric equation for tree species in

112 Japan (Ishihara et al. 2015):

113

$$\ln(y) = -1.196 + 1.162 \times \ln(D) + 0.338 \times (\ln(D))^2$$

$$- 0.044 \times (\ln(D))^3 + 0.708 \times \ln(\rho) \tag{1}$$

114

115 where y is AGB; D is stem DBH, and ρ is the wood specific gravity of each species (Editorial

116 Board of Wood Industry 1966; Kurokawa et al. unpublished; Fujiwara et al. 2007).

117 Confidence intervals of changes in AGB, BA, and stem density were estimated via

118 bootstrapping across 10-m × 10-m quadrats following the method of Valencia et al. (2009).

119   To overview trends in AGB change during the study period and net annual change in

120 AGB, we calculated AGB for three tree size classes: large (≥50 cm DBH), medium (15–50

121 cm DBH), and small (5–15 cm DBH). The net annual change in AGB (in Mg ha^{-1} y^{-1}) was

122 calculated each 4-year period from 1996 to 2019 from the tree DBH data of 1995 to 2019. It

123 was then dissected into annual AGB gain and annual AGB loss. Annual AGB gain was

124 calculated separately for growth of trees in each size class and ingrowth, and AGB loss was

125 calculated for mortality of trees in each size class.

126 **Analysis of factors affecting short-term AGB gain at local scale**

127 We examined the effects of climatic condition in each measurement period, canopy gap

128 formation and topography on local-scale AGB gain using two generalized linear mixed-effect

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129   models (GLMMs). For both models, variables were calculated for every 20-m × 20-m subplot

130   in each 4-year period from 1996 to 2019. Subplot size was determined as an appropriate area

131   to detect gap formation and subsequent recovery in consideration of the range of gap size in

132   KRRF. Both models used AGB gain as the response variable and included subplot as a

133   random effect.

134   In model 1, we aimed to investigate whether the amount of AGB gain differed among the

135   measurement periods with the effects of topographic unit and gap formation in the current and

136   previous measurement periods. Fixed effects were initial AGB in the current measurement

137   period, AGB losses in the current and previous measurement periods, topographic unit, and

138   the five 4-year measurement periods between 2000 and 2019, with topographic unit and

139   measurement period as categorical variables. Initial AGB was included as it is expected to be

140   the "capital" for AGB gain by tree growth. AGB losses were indices of gap formation in the

141   current and previous measurement periods.

142   In model 2, the effect of climate was analyzed separately from the effect of measurement

143   period to avoid multicollinearity. Fixed effects were initial AGB in the current measurement

144   period, AGB loss in the current and previous measurement periods, topographic unit, and

145   mean temperature during the previous autumn (September–November) and the current

146   summer (June–August) over the measurement periods. Both types of mean temperature have

147   a major influence on annual DBH growth of individual trees in most dominant species of

148   KRRF (Matsushita et al. manuscript in preparation). As the on-site temperature data do not

149   cover the entire study period, we used data from the nearest weather station, at Wakayanagi

150   (39°08′N, 141°04′E; 97 m a.s.l.: Japan Meteorological Agency, https://www.data.jma.go.jp/

151   gmd/risk/obsdl/index.php), 18 km east of the study site. These models were fitted by the lme4

152   v. 1.1-21 package (Bates et al. 2015) in R 3.6.3 (R Core Team 2020). To evaluate the variance

153   explained by the models, we calculated two R^2 values for mixed-effect models following the

154   method of Nakagawa et al. (2017): marginal R^2 ($R^2_{GLMM(m)}$), which is the proportion of the

155   variance explained by fixed effects, and conditional R^2 ($R^2_{GLMM(c)}$), which is the proportion of

156   the variance explained by both fixed and random effects. These were calculated by the

157   MuMIn v. 1.43.15 package (Bartoń 2019) in R.

Results

Overall changes in AGB at plot scale

160   BA in 1993 was greatest in the riparian unit (34.2 m² ha⁻¹) and least in the denuded slope unit

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161   (Table 1). From 1993 to 2019, BA increased significantly in all topographic units. AGB was

162   greatest in the terrace unit (246.0 Mg ha^{-1}) at the beginning of the study period (Table 1). It

163   increased significantly in all topographic units during the study period, increasing in most 4-

164   year periods except for some short pauses; for instance, from 2011 to 2015 in the riparian and

165   denuded slope units (Fig. 2). AGB of large trees ($\geq$50 cm DBH) in 1993 occupied 76.7% of

166   total AGB in riparian, 70.6% in denuded slope, and 77.7% in terrace units. Trends of

167   increasing total AGB in the riparian and terrace units were similar to those of large-tree AGB.

168   During the study period, stem density declined in the riparian and terrace units but increased

169   in the denuded slope unit (Table 1). The change in stem density was significant only in the

170   riparian unit.

171   In the riparian unit, *C. japonicum* had the largest AGB at the beginning of the study

172   period, followed by *F. crenata*, *A. turbinata*, *Q. crispula*, and *A. mono* (Table 2). AGB of

173   these species, except for *Q. crispula*, increased during the study period. *Pterocarya rhoifolia*

174   had the greatest increment in AGB over the study period, accounting for 52.3% of the total

175   increment in the riparian unit, followed by *A. turbinata* at 25.4%. In contrast, several other

176   species with relatively small AGB at the beginning, such as *Zelkova serrata* and *Ulmus*

177   *laciniata*, showed a decline in AGB during the study period. The denuded slope and terrace

178   units were dominated by *F. crenata* and *Q. crispula*, and the denuded slope by *A. mono* as

179   well (Table 2). All these species had an increase in AGB during the study period, maintaining

180   the AGB-based rank of species composition.

181   Annual gain in AGB remained at approximately 3 Mg ha^{-1} y^{-1} with some differences

182   among the measurement periods: larger in 2008–2011 and 2016–2019 and smaller in 2004–

183   2007 in all topographic units (Fig. 3). In the riparian and terrace units, large- and medium-

184   sized trees accounted for most of the annual gain. Annual losses in AGB fluctuated among the

185   4-year periods, and were largest in 2012–2015 in all topographic units. Regardless of

186   topographic unit, measurement periods with greater loss of AGB of large trees tended to have

187   greater total loss of AGB. As a consequence, net annual change in AGB ranged from −0.6 to

188   +2.6 Mg ha^{-1} y^{-1} but stayed positive except in 2012 to 2015 in the riparian and denuded slope

189   units.

Effects of climate and gap formation on short-term AGB gain at local scale

191   Local-scale AGB gain in the 20-m × 20-m subplots was positively influenced by initial AGB

192   in each measurement period (GLMM model 1: Table 3, Fig. 4). It was significantly greater in

193   subplots with larger AGB loss in the previous measurement period but smaller in subplots

194   with larger AGB loss in the current measurement period. It was not significantly affected by

195   topographic unit. It differed significantly among the measurement periods: smaller in 2004–

196   2007 and larger in 2008–2011 and 2016–2019. In model 1, $R^2_{GLMM(m)} = 0.31$ and $R^2_{GLMM(c)} =$

197   0.76, indicating that 31% of the variation was explained by fixed effects and 76% by fixed

198   and random effects. In model 2 (Table 4), the effects of initial AGB, AGB loss in the current

199   and previous measurement periods, and topographic unit were almost identical to those in

200   model 1. Local-scale AGB gain was larger in measurement periods with higher mean

201   temperature during the current summer but smaller in those with higher mean temperature

202   during the previous autumn. Model 2 explained almost identical variation as model 1, with

203    $R^2_{GLMM(m)} = 0.32$ and $R^2_{GLMM(c)} = 0.77$.

Discussion

205   AGB of KRRF increased steadily over the 26 years in all topographic units, with increments

206   of 30 to 35 Mg ha^{-1} in each (Table 1). BA also increased over the study period, even though it

207   was initially equivalent to values reported in other cool-temperate old-growth forests in Japan

208   (Masaki et al. 1992; Nakashizuka 1988; Seiwa et al. 2013), indicating that the forest had

209   already been well stocked. These results are consistent with reports that temperate old-growth

210   forests continuously gain biomass over the long term (Keeton et al. 2011; Luyssaert et al.

211   2008). This continuous stand-scale biomass increment was attributable mainly to an increase

212   in AGB of large trees, in agreement with the reported global importance of large trees in

213   determining stand AGB (Lutz et al. 2018; Slik et al. 2013).

214   Patterns of tree growth or stand-biomass-change vary across tree species composition and

215   diversity, as well as with environmental conditions such as topography (Kubota et al. 2004;

216   Valencia et al. 2009). In KRRF, topography was reported to determine tree species

217   distribution through affecting seedling survival differently across species (Masaki et al. 2005).

218   Here, however, a steady increase in AGB was common to all three topographic units (Table 1;

219   Fig. 2), despite the difference in tree species composition among them (Table 2). In addition,

220   local-scale AGB gain did not differ among the topographic units (Table 3). We attribute this

221   similarity to the distinct AGB increment in *F. crenata*, which is dominant in all three

222   topographic units (Table 2). A growing abundance of *F. crenata* is documented in several

223   stable old-growth forest (Seiwa et al. 2013; Yamamoto and Nishimura 1999). Increases in

224   both AGB and stem density of *F. crenata* in KRRF may be due to lack of remarkable

225   disturbance even in the riparian unit during the study period. *Pterocarya rhoifolia*, a riparian

226   specialist of cool-temperate forests in Japan (Sakio et al. 2002), made the largest contribution

227   to the stand AGB increment in the riparian unit (Table 2). Despite the substantial decline in its

228   stem density (Appendix 1), its AGB at the end of the study period was 3 times the initial

229   value. It is likely that the fast growth of *P. rhoifolia* (Sakio 1993) is associated with its rapid

230   increase in AGB. Although AGB decreased in some species such as *Z. serrata* and *U.*

231   *laciniata* in the riparian unit, *P. rhoifolia* compensated for the decrease and resulted in the

232   stand-level AGB increase.

233   Mortality is the major cause of reduced growth or decline in AGB (Schuster et al. 2008;

234   Xu et al. 2012). Although large disturbances such as strong typhoons, insect outbreaks, or

235   severe flooding in the riparian unit were not recorded during the 26 years, the loss of AGB

236   varied substantially among the topographic units and among the 4-year measurement periods

237   (Fig. 3). These variations were explained mainly by the spatio-temporal variation in mortality

238   of large trees. A significant contribution of large-tree mortality to the AGB loss has also been

239   reported in other old-growth forests (Hoshizaki et al. 2004). Despite these temporal and

240   spatial variations, the AGB loss generally remained smaller than the AGB gain, bringing

241   about a positive change in AGB in most of the measurement periods. The temporal change of

242   stand-level AGB appears to be inconsistent with the assumed long-term balance between

243   biomass loss caused by canopy gap formation and subsequent gain during gap recovery.

244   In contrast to AGB loss, temporal fluctuations in AGB gain were generally synchronized

245   across the topographic units at the stand scale (Fig. 3). The results of model 1 indicate that

246   local-scale AGB gain also differed among measurement periods even after adjustment for

247   initial AGB and disturbance during each period (Table 3). As expected, initial AGB positively

248   influenced local-scale AGB gain (Fig.4). Larger AGB loss in the previous measurement

249   period caused greater AGB gain, suggesting that variations in local-scale AGB gain are

250   partially explained by recovery in and around canopy gaps. Local-scale AGB gain also

251   substantially differed among the measurement periods. The results of model 2 suggest that the

252   observed temporal variations in AGB gain are caused by climatic factors: a hotter current

253   summer had positive effects whereas a warmer previous autumn had negative effects on AGB

254   gain (Table 4). The positive response to high temperature in the growing season is consistent

255   with the trends of individual-tree growth observed in deciduous broadleaved species in KRRF

256   (Matsushita et al. manuscript in preparation) and other cool-temperate forests in Japan (Hiura

257   et al. 2019). The negative effect of a warmer autumn on growth is also found in individual-

258   tree growth in KRRF (Matsushita et al. manuscript in preparation) and may be caused by a

259   larger increment in respiration than in photosynthesis (Piao et al. 2008).

260   Our models explained a considerable amount of variation in local AGB gain, although the

261 analysis did not include other potential factors that enhance tree growth such as change in

262 precipitation (Hiura et al. 2019), rising CO_2 levels in the atmosphere (e.g., Norby et al. 2005),

263 and nitrogen deposition (Thomas et al. 2010). The temperature at the weather station nearest

264 to KRRF shows a substantial rise in summer and autumn temperatures over the past 40 years

265 (Appendix 2). Decadal climate trends of warming are likely to have contributed to the

266 observed steady increase in AGB in KRRF by providing favorable conditions for tree growth

267 in the study period. Warming-induced growth acceleration in the past several decades has

268 been reported in temperate and boreal forests in Europe (Kauppi et al. 2014; Pretzsch et al.

269 2014). In Japan, some cool-temperate beech-dominated forests are predicted to be vulnerable

270 to warming (Matsui et al. 2009). Accumulation of tree growth data from a broader range of

271 temperatures across cool-temperate forests in Japan will improve our understanding of the

272 influence of climate change on this type of forest.

Acknowledgements

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Tables

Tables

417 Table 1. Basal area, aboveground biomass, and stem density at the study site at the beginning (1993) and end (2019) of the study period with overall changes in three

418 topographic units (riparian, denuded slope, and terrace).

	1993	2019	Change
Basal area (m^2 ha^{-1})			
Riparian	34.2 (28.7–40.5)	38.6 (32.4–457.7)	4.5 (2.4–6.5)
Denuded slope	21.5 (15.3–28.3)	26.6 (20.2–33.8)	5.1 (2.2–7.8)
Terrace	32.3 (26.6–37.7)	32.3 (26.6–37.7)	4.3 (1.5–6.7)
Aboveground biomass (Mg ha^{-1})			
Riparian	244.1 (202.7–289.4)	274.2 (230.1–326.2)	30.1 (14.0–45.6)
Denuded slope	156.8 (100.3–216.0)	191.5 (136.1–252.7)	34.7 (13.2–56.1)
Terrace	246.0 (202.4–293.5)	276.7 (225.8–336.4)	30.6 (8.0–53.4)
Stem density (stems ha^{-1})			
Riparian	583 (519–648)	509 (452–581)	−73 (−111 to −36)
Denuded slope	781 (637–939)	877 (704–1046)	96 (−35 to 235)
Terrace	952 (833–1061)	906 (785–1031)	−47 (−118 to 24)

419 Values in parentheses are 95% confidence intervals. When CIs do not include 0, the changes are significant.

420 Table 2. Overall changes in aboveground biomass (AGB, in Mg ha^{-1}) of component tree species in each topographic unit during the study period and the relative

421 contribution of each species to the total change in AGB. Species are listed in the order of AGB in 1993 in the entire plot.

Species	Riparian				Denuded slope				Terrace			
	1993	2019	Change	Contribution (%)	1993	2019	Change	Contribution (%)	1993	2019	Change	Contribution (%)
Fagus crenata	52.1	56.2	4.1	13.7	68.9	80.4	11.5	33.2	139.3	153.9	14.7	47.9
Quercus crispula	30.6	30.3	−0.2	−0.8	30.4	37.8	7.4	21.2	82.1	86.3	4.2	13.7
Cercidiphyllum japonicum	58.9	61.9	3.0	10.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Aesculus turbinata	47.8	55.5	7.6	25.4	3.8	5.4	1.6	4.5	0.0	0.0	0.0	0.0
Acer mono	21.0	21.6	0.5	1.8	28.9	38.0	9.0	26.1	0.2	0.4	0.2	0.6
Pterocarya rhoifolia	8.6	24.4	15.8	52.4	0.9	3.7	2.8	8.0	0.0	0.0	0.0	0.0
Zelkova serrata	5.7	4.7	−1.0	−3.2	2.0	3.6	1.5	4.4	0.0	0.0	0.0	0.0
Ulmus laciniata	4.8	2.8	−2.0	−6.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Magnolia obovata	4.2	6.0	1.8	6.1	0.0	0.5	0.4	1.3	1.2	2.2	1.0	3.3
Kalopanax pictus	4.5	5.0	0.5	1.8	0.1	0.7	0.6	1.7	0.0	0.3	0.3	0.9
Acer sieboldianum	0.4	0.1	−0.3	−1.1	4.5	3.5	−1.0	−2.9	6.0	8.0	2.0	6.5
Acer japonicum	0.5	0.9	0.4	1.3	1.9	2.4	0.5	1.5	6.0	7.4	1.4	4.5
Others	5.0	4.8	−0.2	−0.8	15.3	15.7	0.4	1.1	11.2	18.1	6.9	22.5
Total	244.1	274.2	30.1	100.0	156.8	191.5	34.7	100.0	246.0	276.7	30.6	100.0

422

423

424   Table 3. Results of the generalized linear mixed-effect model (model 1) testing the effects of initial aboveground biomass (AGB), canopy gap formation, topographic

425   unit, and measurement period on the AGB gain in 20-m × 20-m subplots.

		Estimate	Standard error	df	t-value	P-value
Intercept		0.259	0.033	148.7	7.868	<0.001
Initial AGB		0.021	0.003	135.8	8.255	<0.001
AGB loss by mortality	Previous	0.016	0.006	511.7	2.819	0.005
	Current	−0.017	0.006	481.0	−2.782	0.006
Topographic unit	Denuded slope	0.023	0.047	109.3	0.501	0.618
(v. Riparian)	Terrace	−0.018	0.039	109.0	−0.461	0.646
Measurement period	2004–2007	−0.050	0.015	442.1	−3.301	0.001
(v. 2000–2003)	2008–2011	0.038	0.015	445.1	2.514	0.012
	2012–2015	−0.005	0.015	450.5	−0.327	0.743
	2016–2019	0.040	0.015	455.9	2.606	0.009

426

427

428　Table 4. Results of the generalized linear mixed-effect model (model 2) testing the effects of initial aboveground biomass (AGB), canopy gap formation, topographic

429　unit, and climate (mean air temperature) of each measurement period on the AGB gain in 20-m $\times$ 20-m subplots.

		Estimate	Standard error	df	t-value	P-value
Intercept		−0.559	0.321	445.1	−1.738	0.083
Initial AGB		0.021	0.003	137.9	8.294	<0.001
AGB loss by mortality	Previous	0.016	0.006	508.0	2.925	0.004
	Current	−0.015	0.006	481.7	−2.550	0.011
Topographic unit	Denuded slope	0.023	0.047	109.4	0.498	0.619
(v. Riparian)	Terrace	−0.018	0.038	109.1	−0.462	0.645
Mean air temperature	Previous autumn	−0.137	0.023	443.0	−5.865	<0.001
	Current summer	0.120	0.021	450.8	5.803	<0.001

430

Figure legends

431

432 Fig. 1. Topographic map of the Kanumazawa Riparian Research Forest (KRRF). The solid frame
433 represents the 4.71-ha KRRF plot. Colors denote the three topographic units: blue, riparian (3.11 ha);
434 orange, denuded slope (0.57 ha); green, terrace (1.06 ha). Black dotted lines show the 10-m × 10-m
435 quadrats; thin red lines show the 20-m × 20-m subplots. Contour interval is 2 m.

436 Fig. 2. Trends in total aboveground biomass (AGB) over 26 years in the three topographic units. AGB is
437 shown for stand total and stems in three size classes: large (diameter at breast height [DBH] $\geq$ 50 cm),
438 medium (DBH, 15–50 cm), and small (DBH, 5–15 cm).

439 Fig. 3. Components of average annual change in aboveground biomass (AGB) by each measurement period
440 in the three topographic units. Blue bars (4 levels of color gradient) denote annual AGB gain from growth
441 of surviving stems in the three size classes (large, diameter at breast height [DBH] $\geq$ 50 cm; medium, 15–
442 50 cm DBH; small, 5–15 cm DBH) and ingrowth. Orange bars (3 levels of color gradient) denote annual
443 AGB loss from stems that died during each measurement period in the three size classes. Dark gray bars
444 denote net average annual change in AGB.

445 Fig. 4. Local-scale aboveground biomass (AGB) gain per 4-year measurement period in relation to initial
446 AGB of measurement period. Colors represent classes of AGB loss in previous measurement period;
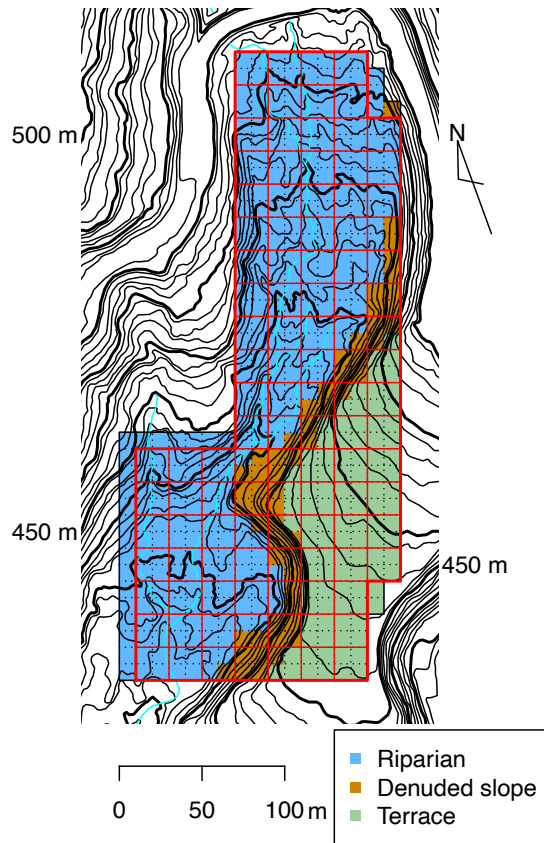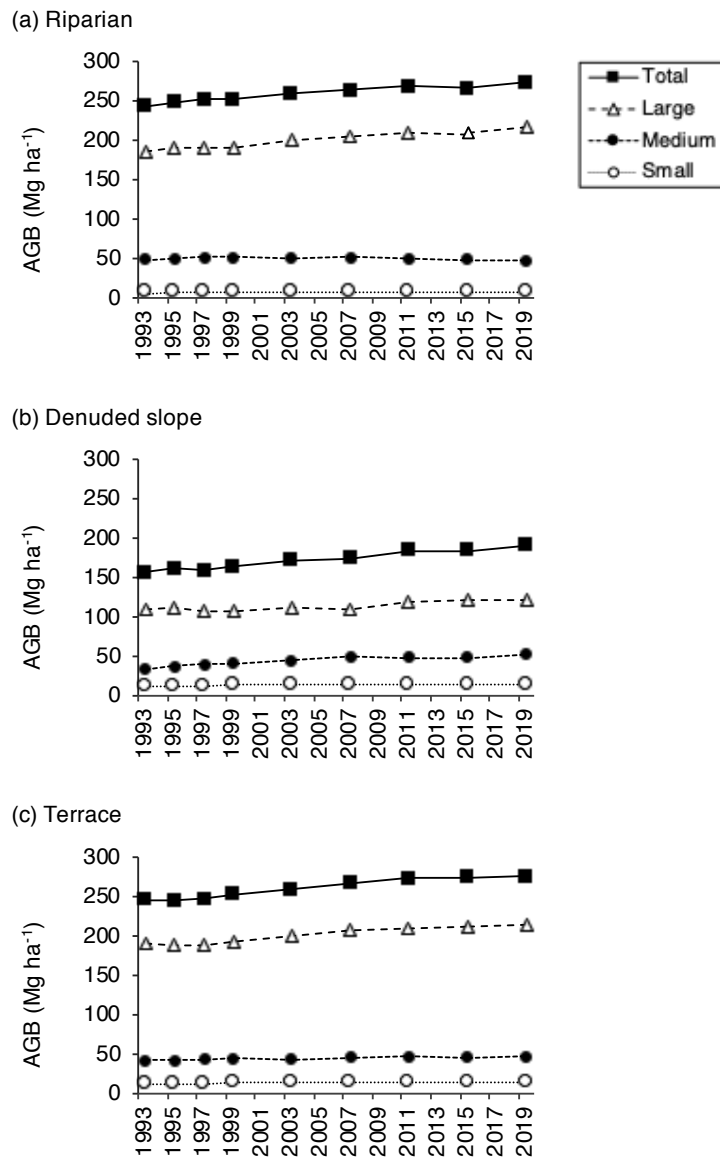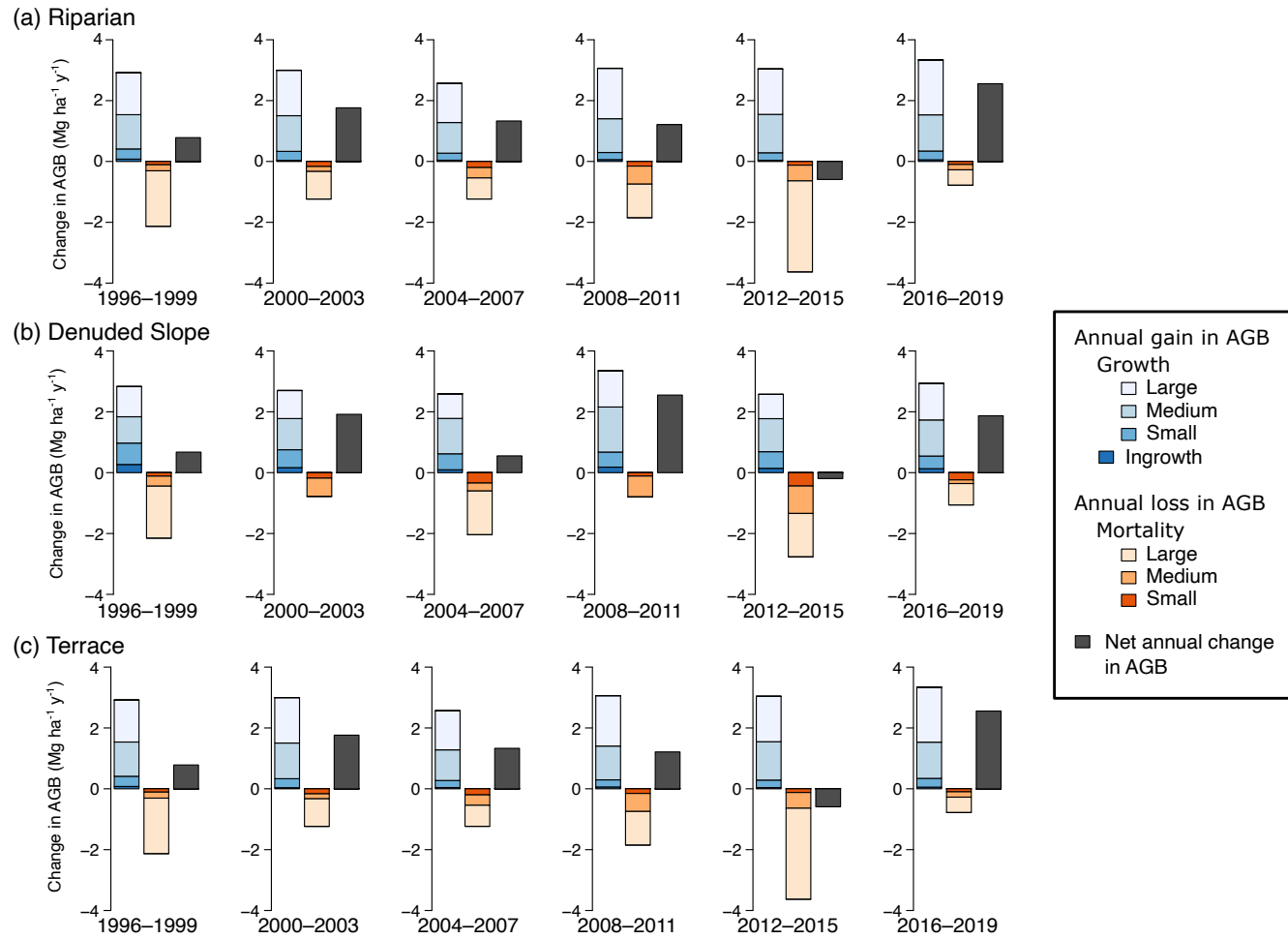447 symbols represent measurement periods.

Fig. 1

Fig. 2

(a) Riparian

(b) Denuded slope

(c) Terrace

Fig. 3

(a) Riparian

Change in AGB (Mg ha⁻¹ y⁻¹)

1996–1999   2000–2003   2004–2007   2008–2011   2012–2015   2016–2019

(b) Denuded Slope

Change in AGB (Mg ha⁻¹ y⁻¹)

1996–1999   2000–2003   2004–2007   2008–2011   2012–2015   2016–2019

(c) Terrace

Change in AGB (Mg ha⁻¹ y⁻¹)

1996–1999   2000–2003   2004–2007   2008–2011   2012–2015   2016–2019

Annual gain in AGB
Growth
☐ Large
☐ Medium
☐ Small
☐ Ingrowth

Annual loss in AGB
Mortality
☐ Large
☐ Medium
☐ Small

☐ Net annual change
   in AGB

Fig.4