Variation in tree diameter growth in response to the weather conditions and tree size in deciduous broad-leaved trees

Eri Nabeshima [a,*], Takuya Kubo [b], Tsutom Hiura [a]

[a] Tomakomai Research Station, Field Science Center for Northern Biosphere, Hokkaido University, Takaoka, Tomakomai 053-0035, Japan
[b] Division of Bioscience, Graduate School of Environmental Earth Science, Hokkaido University, Kita 10 Nishi 5, Sapporo 060-0810, Japan

ARTICLE INFO

ABSTRACT

The diameter growth of trees may vary depending on the tree size, species and other tree-related factors. However, such variation is challenging to consider while estimating the growth response to weather conditions. This study investigated the effects of the weather conditions and variations in tree factors on diameter growth in a mature forest. In particular, we focused on diameter growth in June, the month of active diameter growth. We recorded the monthly diameter growth of 6 tree species for 7 years and constructed a generalized linear mixed model in which the mean growth was dependant on tree size, weather conditions, and the interaction between tree size and weather.

The estimated growth responses to weather factors were different among species, but their interaction to tree size was unclear in all species. Sensitivity analysis of growth rate to weather conditions, such as temperature and precipitation, showed that the sensitivity to weather depended both on tree size and tree species.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

It is now recognized that the change in climate conditions can remarkably affect forest productivity at biome or regional level (Houghton et al., 2001). Tree diameter growth is commonly used for estimating aboveground carbon sequestration in forest, from direct measurement (Hiura, 2005) or tree rings (Hogg and Wein, 2005). To reveal how tree diameter growth responds to weather condition would help us understand the biological mechanisms of forest carbon storage, as there is an argument that the estimate of interannual variability of net ecosystem production based on eddy covariance technique is mostly responsible for that of aboveground woody growth (Ohtsuka et al., 2009). However, diameter growth simultaneously depends on the tree characteristics (e.g., age, size and competition status), microenvironment (e.g., light and nutrient availability), and species. Such variations make it difficult to elucidate the weather effects on tree diameter growth, especially in natural forest stand having trees of various sizes and diverse species.

Relationships between tree diameter growth and weather have been well investigated using dendrochronology (Cook and Kairiukstis, 1990; Yasue et al., 1996; Rigling et al., 2002; Takahashi et al., 2003; Saurer et al., 2004; Briffa et al., 2008; St. George et al., 2008). In order to detect the growth fluctuation in trees caused by weather conditions, these studies minimize the variations among trees (e.g., tree age, competition status, or microenvironment), by conducting measurements in an even-aged stand, selecting open grown trees, or using statistical techniques (Fritts, 1976). In addition, it is generally assumed that the growth in response to the weather is independent of tree size (Carrer and Urbinati, 2004). However, recent theoretical and ecophysiological studies suggest that functional processes strongly coupled to tree growth are closely associated with their size (Hubbard et al., 1999; Enquist, 2002; Midgley, 2003; McDowell et al., 2005; Nabeshima and Hiura, 2007) rather than with their age (Mencuccini et al., 2005; Matsuzaki et al., 2005; Bond et al., 2007). For example, "hydraulic limitation hypothesis" explains that the leaf photosynthetic rate declines with tree size in some pine species because the water transport from root to leaves becomes more difficult in larger trees owing to their extended conducting systems (Ryan and Yoder, 1997; Hubbard et al., 1999). This implies that the magnitude and direction of the weather effects on the plants can be modified by their size.

In addition to growth variation and size dependency, the growth response to weather *per se* is the outcome of complex physiological phenomena. Although there are many studies that investigated relationships between observed weather conditions and measured tree diameter growth, from tree rings (Cook and Kairiukstis, 1990; Yasue et al., 1996; Rigling et al., 2002; Takahashi et al., 2003; Saurer et al., 2004; Briffa et al., 2008; St. George et al., 2008) or direct growth measurements (McLaughlin et al., 2007;

* Corresponding author. Present address: Tokyo University of Agriculture and Technology, 3-8-1, Harumi-cho, Fuchu 183-8538, Japan. Tel.: +81 43 277 2292; fax: +81 43 277 2292.
E-mail address: nabeshima.eri@gmail.com (E. Nabeshima).

Laubhann et al., 2009), only a few studies have presented growth models that are based not only on empirical data but also on physiological processes in order to reveal causal relationships between weather and tree growth (Berninger et al., 2004). Because physiological models typically have a complex structure and many parameters, it is technically difficult to determine such models statistically with growth measurements (Korzukhin et al., 1996). On the other hand, it is suggested that empirical models are more realistic but less sensitive to changing environment than physiological models (Matala et al., 2003).

In order to model tree growth to weather conditions with the physiological processes, we have to start with the differences between physiological processes in the response time to weather conditions. For example, the effects occurring via metabolism (e.g., cell division and growth depending on temperature and water availability at the moment) are immediate, while the effects occurring via the mechanisms of photosynthesis can be delayed when photosynthetic products are stored and used as materials for growth in the subsequent years. Several studies suggest that diameter growth in springtime depends on stored photosynthates assimilated in the previous year, while diameter growth in summertime depends on photosynthetic production by newly developed leaves (Kienholz, 1934; Ishizuka, 1981; Gough et al., 2008). The resulting delayed growth responses to climatic factors, such as monthly temperature and precipitation, have been repeatedly reported by dendrochronological studies (e.g., Yasue et al., 1996).

Another difficulty in modelling tree growth with consideration of physiological phenomena is that different weather factors have a multiplicative rather than additive effect on plant growth. This is because plant growth and photosynthesis require a balanced combination of favorable conditions (e.g., temperature and humidity) and essential resources (e.g., light, water, and nutrients) (Bloom et al., 1985). Moreover, nonlinearity is widespread in the case of the response of plant photosynthesis and growth to weather factors. For example, the photosynthetic rate is a saturating function of light intensity and a unimodal function of temperature (Hikosaka, 1997). Further, a dendrochronological study reported a possible nonlinearity in the growth response to temperature (Daniels and Veblen, 2004). Nevertheless, few studies adequately consider nonlinearities as well as the time lag in the response of the diameter growth to the weather conditions.

The effects of weather and tree size on growth may vary among different species. The optimal temperature for photosynthesis and/or growth is different among species occupying different habitats, and the optimal light intensity differs among successional forest types (Lambers et al., 1998). Kohyama et al. (2003) analyzed the relationship between tree size and growth rate and found that as the diameter increases the diameter growth rate decreases, there is a negative correlation between the rate of the growth deceleration and the maximum tree height in the case of each species.

This study investigated the effects of weather conditions on the growth of trees considering several variations, such as the tree size and species. We addressed the following issues: (1) how the immediate and delayed responses to weather conditions contribute to the annual variation in tree growth, (2) how tree size modify growth responses to weather variation, and (3) whether these responses differ between species.

2. Materials and methods

2.1. Study site and study trees

The study sites were mature deciduous broad-leaved forest stands in Tomakomai Experimental Forest (TOEF, 42°40′N,

141°36′E) on the island of Hokkaido, Japan. The annual precipitation at TOEF was 1177 mm year^{-1} and the precipitation in summer was 182 mm month^{-1}. The summer and winter mean temperatures were 17 °C and −4 °C, respectively. The topsoil of the study site was very shallow and the volcanic deposits of Mt. Tarumae, which erupted in 1667 and 1739, are about 2 m thick (Shibata et al., 1998). The study species were *Acer mono* var. *glabrum*, *Acer amoenum*, *Ostrya japonica*, *Carpinus cordata*, *Magnolia obovata*, and *Quercus crispula*, which are major species at the study site (Hiura et al., 1998). These species are diffuse-porous trees, except for *Q. crispula*, which is ring-porous (Table 1). They are mid- to late-successional species and the asymptotic height is larger in the case of *A. mono*, *Q. crispula*, and *O. japonica* than in the case of other species (Table 1). In March 1998, we installed dendrometer bands on trees with a diameter at breast height (DBH) greater than 10 cm in a 1 ha plot as well as on some trees in an adjacent forest stand in February 2001 in order to increase the number of samples and to extend the range of DBH. The dendrometer band is made of aluminium and manually read; it has a measurement accuracy of 0.1 mm DBH (Liming, 1957). We recorded the growth of these trees every month, from the second month after installation of the dendrometer band until November 2004. We confirmed that the trees in this study reasonably represent the maximum size of each species (Hiura et al., 1998; Hiura, 2005; Nabeshima, 2005).

In this study, we focused on the diameter growth in June. The diameter growth of the trees in the cool temperate forest in the northern hemisphere occurs mainly from June to July (Imagawa and Ishida, 1970), and the diameter growth in June at our study site strongly correlated with the annual diameter growth (the correlation coefficients of the 6 studied species ranged from 0.75 to 0.88) (Nabeshima, 2005). Although the trees may often exhibit a delayed growth response to the weather conditions due to the stored photosynthetic products, it is difficult to determine how and when this delayed growth response occurred (Helle and Schleser, 2004). In our study site, bud break in the trees generally begins in late May, and the photosynthetic rates of the studied species were still low in June (Shimizu et al., unpublished). Therefore, the photosynthetic products in May and June of the current year probably would not affect the ring growth in June. For this reason, we assumed immediate and delayed growth responses to weather conditions that the weather in June of the current year directly affected the growth in June via the metabolism mechanism during cell growth while the weather conditions in the previous year affect the June growth via the stored photosynthetic products. The yearly changes of mean diameter growth in June are shown in Fig. 1. Although diameter growth in July also highly correlated with the annual diameter growth (0.86–0.96), the yearly changes of mean growth in July were more stable (for *A. mono*, *A. amoenum*, and *Q. crispula*) or similarly fluctuated (for *O. japonica*, *C. cordata*, and *M. obovata*) compared to those in June growth. In addition, diameter growth

Table 1
The structural and life historical traits of six studied species (Koike, 1988, Nabeshima, 2005).

	Successional status	Xylem structure	Asymptotic[a] height (m)
Acer mono	Late	Diffuse	22.16
Acer amoenum	Late	Diffuse	19.91
Ostrya japonica	Mid	Diffuse	25.64
Carpinus cordata	Late	Diffuse	15.98
Quercus crispula	Mid	Ring	22.58
Magnolia obovata	Mid, gap-phase	Diffuse	18.62

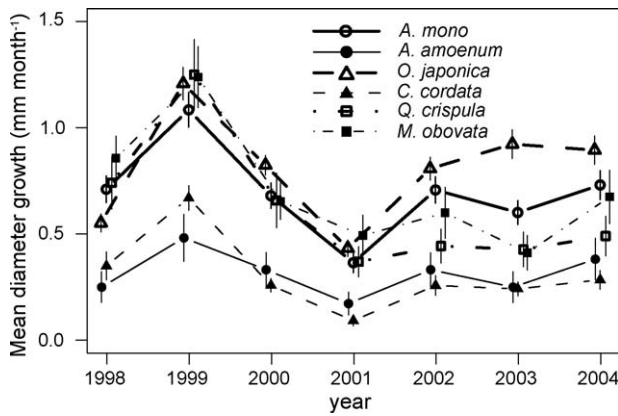[a] Asymptotic heights were estimated using Eq. (2) in Thomas (1996).

Fig. 1. The yearly changes of mean diameter growth in June. Bars indicate standard error.

in July would be affected by the leaf photosynthetic products during the same time (i.e., July) of the current year, which makes the structure of the growth model even more complicated. As it is difficult to estimate the models with more numbers of parameters, we did not use July growth but June growth for the analysis of this study.

2.2. Weather data

Weather data were measured hourly at a research tower in TOEF. The following variables were measured: temperature (1.5 m high) (platinum resistance thermometer, E-734; Yokogawa Weathac, Inc., Tokyo, Japan), relative humidity (19 m high) (electrostatic capacity hygrometer, P-HMP-45D, Ogasawara Keiki Seisakusho, Tokyo, Japan), precipitation (tipping-bucket rain gauge, B-011; Yokogawa Weathac, Inc., Tokyo, Japan), and photosynthetic photon flux density (32.5 m high) (photosynthetically active radiometer, ML-020P; EKO Inc., Tokyo, Japan). Vapour pressure deficit (V) was calculated using relative humidity and temperature by the following equation (Jones, 1992):

$$V = 0.61375 \exp\left[17.502\frac{T}{T + 240.97}\right](1 - H),\qquad(1)$$

where T is the hourly temperature and H is the hourly relative humidity. Missing data were complemented with a dataset from a local meteorological station that conducts hourly measurements in Tomakomai City of the Japan Meteorological Agency (42°37.3′N, 141°32.8′E, 6.3 m elevation, ca. 6000 m distant from TOEF). Weather data in TOEF were regressed to the weather data at Tomakomai City. The estimated equations for temperature,

vapour pressure deficit, and precipitation are as follows:

$$T_e = -1.927 + 1.163T_{toma} - 0.005810T_{toma}^2,\qquad(2)$$

$$V_e = \exp[-0.003726 + 0.9376\log(V_{toma} + 1)] - 1,\qquad(3)$$

$$P_e = 0.9337P_{toma},\qquad(4)$$

where T_{toma}, V_{toma}, and P_{toma} are the data of temperature, precipitation, and vapour pressure deficit at Tomakomai, respectively, and T_e, V_e, and P_e are estimations of temperature ($R^2 = 0.95$, $p < 0.001$), vapour pressure deficit ($p < 0.001$), and precipitation ($R^2 = 0.95$, $p < 0.001$), respectively. The missing data of T_{toma}, V_{toma}, and P_{toma} were complemented with T_e, V_e, and P_e. Note that the data of photosynthetic photon flux density (PPFD) was not missing. The complemented data were averaged per day (for T_{toma} and V_{toma}) or integrated to daily values (for P_{toma} and PPFD) for analysis (Table 2).

2.3. Modelling

2.3.1. Generalized linear mixed model

We constructed a growth model of which set of the factors for the fixed effects is consist of weather conditions in current and previous years, tree size, and other variations to compare the growth among the species. Because we measured the diameter growth a number of times for each tree, time autocorrelation caused by repeated measurement from identical trees should be considered. Therefore, we also took into account "individual variability" as a random effect in the modelling of tree growth to represent the tree-specific response (Crawley, 2005). The models including such random effects are effective for analyzing longitudinal in time or nested data and have recently been used in forest research (Calama and Montero, 2004; Zhao et al., 2005).

In order to separate the effects of tree size and weather factors on DBH growth considering the unobserved characteristics for each tree, a generalized linear mixed model (GLMM), including both fixed and random effects, was applied to the DBH growth data for parameter estimation. The response variable of the model is $G_{i,y}$; DBH growth of an individual i in June of year y. As the measuring precision of DBH growth measurements is 0.1 mm, the set of the random variables of DBH growth, $\{G_{i,y}\}$, is converted into a count dataset in which $G_{i,y}$ is the number of 0.1 mm growths in June.

We assume that $G_{i,y}$ follows a compound Poisson distribution, in which the mean depends on the fixed effects and the variance is modified by the random effects. By adopting the Poisson distribution to represent the variation in diameter growth, we can model "zero growth" which appears frequently in the growth data. Hence, we do not use log transformed diameter growth because the probability of zero growth is always zero in all log transformed distributions.

Table 2

The summary (average and SD in parentheses) of weather factors observed in TOEF. Note that missing data were complemented with a dataset from a local meteorological station in Tomakomai City.

Year	Previous years[a]			Current years[b]	
	Temperature (°C)	VPD (kPa)	PPFD (mol m^{-2} day^{-1})	Temperature (°C)	Precipitation (mm day^{-1})
1998	15.98 (3.33)	0.288 (0.223)	26.22 (15.04)	12.19 (2.93)	3.30 (8.71)
1999	16.38 (3.20)	0.367 (0.198)	25.48 (15.46)	14.34 (1.71)	2.00 (6.55)
2000	18.02 (3.72)	0.479 (0.226)	31.25 (14.47)	14.25 (2.02)	3.30 (11.46)
2001	17.57 (3.03)	0.371 (0.224)	28.34 (15.35)	13.47 (2.70)	1.23 (3.47)
2002	15.84 (3.15)	0.355 (0.193)	27.40 (14.77)	12.72 (1.82)	2.10 (6.88)
2003	15.55 (2.98)	0.332 (0.210)	25.38 (14.27)	13.39 (2.23)	3.60 (8.65)
2004	15.25 (2.59)	0.317 (0.196)	25.93 (14.10)	13.84 (1.48)	2.41 (6.45)

[a] Weather factors from June to September in previous years.

[b] Weather factors of June in current years.

The fixed effect terms include size (logarithm of DBH) and weather terms, and the interactions between size and weather. Since we employ the log link function which is the canonical link function for the Poisson family (Crawley, 2005), the mean growth rate is defined as,

$$\log \lambda_{i,y} = a_0 + a_1 D_{i,y} + a_2 D_{i,y}^2 + (a_3 + a_4 D_{i,y})W_y^P + (a_5 + a_6 D_{i,y})W_y^C,$$ (5)

where $\lambda_{i,y}$ is the mean growth rate of the individual i in June of year y; $a_0, \ldots, a_6$ are the parameters to be estimated; $D_{i,y}$ is the size (logarithm of DBH) of individual i in year y; W_y^P and W_y^C are the weather indices for the previous and current years respectively (defined in the next subsection).

The random effects representing individual-specific response to DBH growth do not change the population median of growth rate but increase its variance (Crawley, 2005). Incorporating the random effects into the tree growth model is required because the heterogeneity among the trees in the observed population cannot be neglected; furthermore, in the modelling of longitudinal data in which multiple replications are obtained from identical trees, these terms is essential (Crawley, 2005). The possible sources of the random effects in the tree growth data are unobserved factors affecting growth rate such as tree age, genotype, local topography, and light environment. We assume that the random effects are constant during the observation period (1998–2004) for simplicity.

Note that we preliminary tested the model having "competition status", an index of light environment, as fixed effects, however, the model were not chosen by model selections using Akaike's Information Criterion (AIC; Akaike, 1973). Competition status were evaluated the sum of basal area of larger trees than the focal tree in the same 2.5 m by 2.5 m grid and in the adjacent grid for each tree.

The gamma distribution is chosen as the distribution of random effects on growth rate because this is the conjugate prior for the Poisson distribution (Gelman et al., 2004). We assume that the random effects of tree i, r_i, follows the gamma distribution with mean 1 and variance s^2. The variance parameter s for random effects is also the parameter to be estimated from the observation. By taking into account both fixed and random effects, the DBH growth of tree i follows the Poisson distribution with intensity $r_i \lambda_{i,y}$. In GLMM, the likelihood is evaluated by taking the expectation for all possible r_i for all individuals, that is, r_i is integrated out in the likelihood equation. The details of the likelihood equation for the model are described in Appendix A.

2.3.2. Modelling weather index

Weather factors such as air temperature and precipitation are confounding and correlated, therefore, many synthesis techniques have been proposed to summarize them by multivariate statistics (e.g., Yeh and Wensel, 2000). These conventional methods of modelling weather factors are based on weighted linear summation of weather measurements. Although these methods make calculation easy, the interpretation of the results in an ecological context is sometimes difficult. To address this problem, we introduced a new "weather index" to integrate the weather factors into an index that forms part of the fixed effects of the tree growth model. The weather index is designed such that it takes into account both the nonlinear responses of trees to weather factors and the intersection effects of these responses.

Our weather index is defined as the sum of the product of the filtered weather measurements for each observation year. Suppose that we have a set of 3 types of weather measurement series, {$x_{1,y}(d)$, $x_{2,y}(d)$, $x_{3,y}(d)$}, at day d in year y and a set of nonlinear weather filters, {$f_*(x)$}, corresponding to each $x_{*,y}(d)$ and the weather index for year y would be defined as

$$W_y = \sum_d f_1(x_{1,y}(d)) \times f_2(x_{2,y}(d)) \times f_3(x_{3,y}(d)),$$ (6)

where every weather filter normalizes its weather measurement ranged from 0 to 1. In case that all the weather filters are designed such that they provide larger values under "better" weather conditions, the weather index W_y would represent the total number of "good" days of tree growth in year y. The functional forms and parameters of the weather filters are estimated based on weather and tree growth data.

The tree growth in June could depend not only on the weather factors in the current year (y) but also on those of the previous year ($y - 1$). We assume that the weather conditions in the previous year affect June growth through the stored photosynthates, while weather conditions in the current year affect growth via metabolism, e.g., the cell division rate. On the basis of these findings, we believe that the weather index, W^P, for the year previous to y should be evaluated only in summer, from June to September during the leafing period (Shimizu unpublished) and that for the current year y, W^C, evaluated only in June.

We selected weather measurements to plug into the growth model from among those that possibly affect tree growth and photosynthesis. Light is the energy required for the photosynthetic reaction, while a vapour-pressure deficit limits photosynthesis through the decline of stomatal conductance (Tenhunen et al., 1985; Ishida et al., 1999). Temperature acts on metabolism and photosynthesis through the activation of enzymes. Precipitation may affect diameter growth and photosynthesis through the availability of water for trees (Tabuchi and Takahashi, 1998). The function forms of the weather filters for these weather data were preliminarily chosen by the model selections using Akaike's Information Criterion (Akaike, 1973) to determine which weather factors were more influential on diameter growth in the growth model.

Based on the goodness of fit to the growth data, the functional forms of weather indices are defined as follows and the some examples of our nonlinear weathers filters are shown in Fig. 2. The photosynthetic weather index for year y, W_y^P, depends on the temperature (x_t), photosynthetic photon flux density (x_f) and vapour pressure deficit (x_v) in the previous year ($y - 1$),

$$W_y^P = \sum_d T_P(x_t(d)) \times F(x_f(d)) \times V(x_v(d)),$$ (7)

where the functional forms of its weather filters are,

$$T_P(x_t(d)) = \exp \frac{-(x_t(d) - a_{tp1})^2}{a_{tp2}^2},$$ (8)

$$V(x_v(d)) = \exp(-a_v x_v(d)),$$ (9)

$$F(x_f(d)) = 1 - \exp(-a_f x_f(d));$$ (10)

T_P, V, and, F are the functions of temperature, vapour pressure deficit, and photosynthetic photon flux density, respectively; a_{tp1} (best of T_P), a_{tp2} (width of T_P), a_v, and a_f are the parameters to be estimated.

The metabolism weather index for year y, W_C, depends on the temperature (x_t) and smoothed precipitation ($\bar{r}$) in the current year (y).

$$W_y^C = \sum_d T_C(x_t(d)) \times P(\bar{r}(d)),$$ (11)
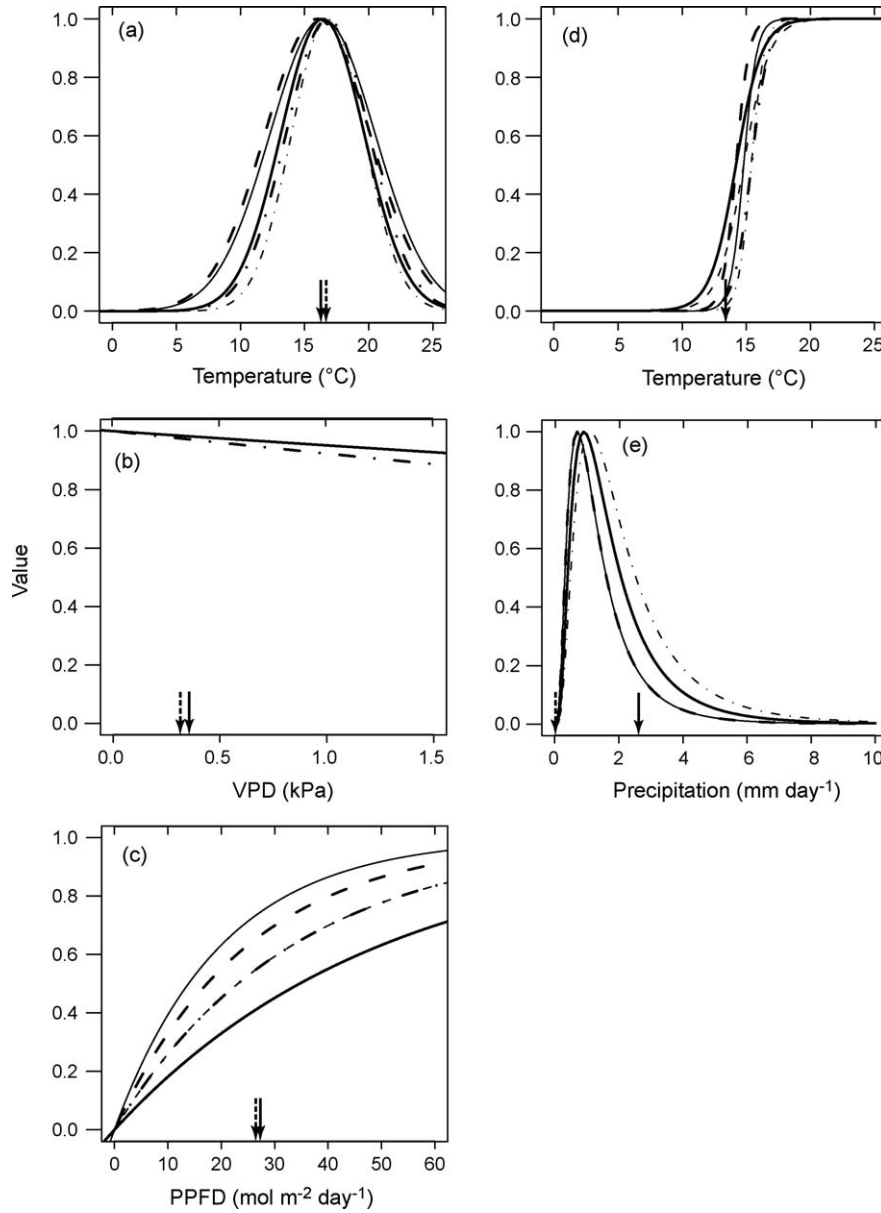
Fig. 2. Selected weather filters for each species. Each y-axis represents the responses to weather factor. (a–c) Weather factors in the previous year; and (d and e): weather factors in the current year. The estimated parameter values are shown in Table 3. Lines are as in Fig. 1. Arrows indicate the mean (solid line) or median (dotted line) of weather conditions during observation (Table 2). Note that two arrows overlap with each other in figure (d).

where the functional forms of its weather filters are,

$$T_C(x_t(d)) = \frac{1}{1 + \exp[-(x_t(d) - a_{tc1})a_{tc2}]}, \tag{12}$$

$$P(\bar{r}(d)) = \exp\left[-\log\left(\frac{\bar{r}(d)}{a_{r1}}\right)^2\right], \tag{13}$$

T_C and P are the functions of temperature and precipitation, respectively; a_{tc1} (centre of T_C), a_{tc2} (slope of T_C), and a_{r1} are the parameters to be estimated. The smoothed precipitation, $\bar{r}(d)$, used above is defined as a weighted and moving average to consider the influence of rainfall on date d and on the days before d,

$$\bar{r}(d) = \sum_{\Delta d} (1 - a_{r2})^{\Delta d} r(d - \Delta d), \tag{14}$$

where Δd is in the range from zero to a value large enough to neglect the influence of past rainfall; a_{r2} is the discounting rate of

the effect of past; $r(d)$ is the precipitation fall on date d. The derived weather indices were shown in Fig. 3.

2.3.3. Parameter estimation and sensitivity analysis

The parameters of the GLMM for fixed, random effects, and weather filters were estimated by the numerical maximum likelihood method (Table 3) (the likelihood equation is provided in Appendix A). The details to obtain and select the estimates for the fixed effects ($\{a_0, \ldots, a_6\}$), random effects (s), and weather filters are described in Appendix B. Size dependency of estimated mean diameter growth for each species as well as of measured diameter growth for each tree was shown in Fig. 4. Fig. 5 shows estimated diameter growth for each tree against measured diameter growth.

In order to compare the growth responses to weather factors among the tree species, we carried out a sensitivity analysis for the estimated growth model that shows the response gradient of mean DBH growth to a small change in weather factors, including the
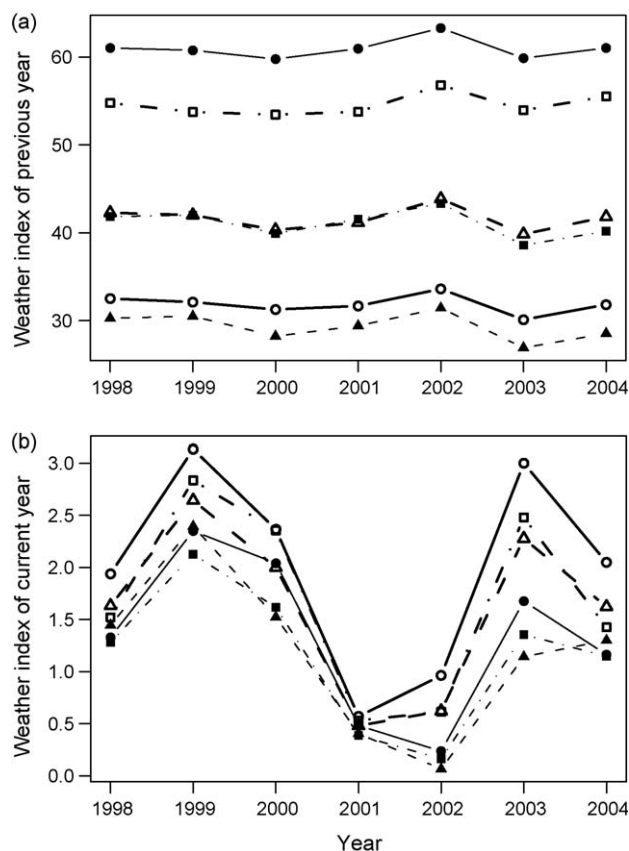
Fig. 3. The yearly changes in weather indices of (a) previous and (b) current years. Symbols and lines are as in Fig. 1.

size dependencies (Fig. 6). Let λ be the mean growth rate for a species depending on size and weather in terms of which the coefficients are estimated with GLMM from the field measurements. We assume that λ is the function of a weather index, W, that depends on a weather factor x. The sensitivity of the mean growth rate λ to weather factor x was defined as

$$\frac{\partial \lambda}{\partial x} = \frac{\partial \lambda}{\partial W} \cdot \frac{\partial W}{\partial x}. \tag{15}$$

From the first component on the right hand side, we obtain the relationship $\partial \lambda / \partial W = \hat{a}_W \lambda$, where $\hat{a}_W$ is the estimate of the coefficient for W because the functional form of λ (in Eq. (5)) is exponential. Therefore, the sensitivity is proportional to the mean growth rate. Since the second component, $\partial W / \partial x$, could not be

analytically treated, we evaluated it using numerical differentiation method.

3. Results

The yearly changes in diameter growth in June were different among species (Fig. 1), although the mean growth of these species was similarly high in 1999 and lower in 2001. The estimated weather filters were also different among species (Table 3, Fig. 2). The optimal temperature in the previous year was higher in Q. crispula and M. obovata, while the width of the filter function of temperature in the previous year was broader in the case of A. amoenum and O. japonica (Fig. 2a). The filter of vapour-pressure deficit was similar among species, except that in the case of Q. crispula, it declined more steeply (Fig. 2b). The filter function of photosynthetic photon flux density (PPFD) was less steep in the case of A. mono and M. obovata (Fig. 2c). The central parameter of temperature in the current year was lower in the case of A. mono and O. japonica (Fig. 2d). The optimal value of precipitation was lower in the case of A. amoenum and O. japonica and higher in M. obovata (Fig. 2e).

The yearly changes in the weather indices in the previous and current years were different (Fig. 3). These patterns also differed from those of growth (Fig. 1). Although the patterns of the previous year were similar among species, those of the current year were likely to differ among species, especially in the years from 2001 to 2002.

The total AIC of estimated growth models was smaller than the AIC of the model that ignores the species (5470.6 and 5535.2, respectively). Diameter growth depended on DBH in A. mono, O. japonica, Q. crispula, and M. obovata (Table 3, Fig. 4). The growth of O. japonica increased with DBH, while in the other three species the growth initially increased and then declines with increasing DBH. The decline in the case of M. obovata set in when the tree size was smaller compared to that in the other two species. In contrast to these four species, diameter growth of A. amoenum and C. cordata were not dependent on DBH (Table 3, Fig. 4). The interaction terms between tree size and climatic factors were not selected in any species (Table 3).

Fig. 5 shows the relationships between the measured and predicted diameter growth for each tree. The predictions are the expectations for each tree and year. In the growth model, the combination of both weather indices in the previous and current years successfully explained the yearly changes in diameter growth in June for each species (Table 3).

The results of the sensitivity analysis are shown in Fig. 6. The sensitivity to temperature was likely to be higher in current year than in previous year. With regard to the responses of the 6 species

Table 3
Estimated parameters of weather filters and generalized linear mixed models.

	Weather filter[a]						Generalized linear mixed model						Sample[b]	
	Previous year				Current year		Fixed					Random	n_i	n_g
	T_P		V	F	T_C		P	a_0	D	D^2	W^P	W^C	scale.log[c]		
	a_{tp1}	a_{tp2}			a_{tc1}	a_{tc2}									
A. mono	16.4	4.6	0.05	0.02	14.2	1.0	0.9	−12.256	3.194	−0.421	0.241	0.353	−0.835	69	405
A. amoenum	16.4	5.8	0.05	0.05	14.8	2.0	0.7	−18.243	–	–	0.304	0.554	1.049	22	151
O. japonica	16.0	5.8	0.05	0.04	14.2	2.0	0.7	−13.401	0.872	–	0.213	0.422	−1.924	40	234
C. cordata	16.4	4.6	0.05	0.03	14.8	1.0	0.9	−14.246	–	–	0.336	0.785	−0.970	26	140
Q. crispula	16.8	4.6	0.08	0.03	15.4	1.5	0.9	−13.913	4.645	−0.628	0.165	0.599	−0.969	23	124
M. obovata	16.8	4.0	0.05	0.02	15.4	2.0	1.1	−15.269	7.342	−1.123	0.172	0.413	−0.284	29	149

Note. The interactive effects of tree size and weather index ($D \cdot W^P$ and $D \cdot W^C$) in generalized linear mixed models are not shown because these parameters did not selected in any of the studied species.
[a] See Eqs. (7)–(14) and Eq. (5) for the functions of weather filters and generalized linear mixed models, respectively.
[b] Numbers of tree individual (n_i) and numbers of growth (n_g) used in each estimation.
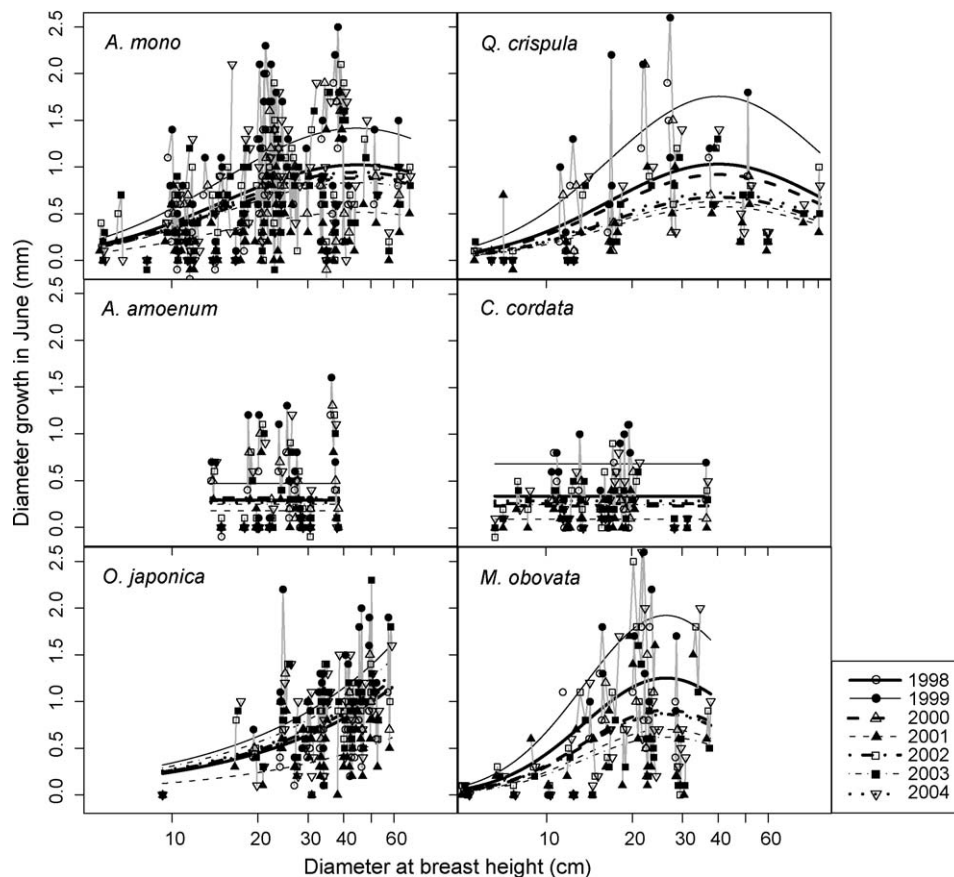[c] Individual variability in log scale.

Fig. 4. Relationships between diameter at breast height (DBH) and monthly diameter growth in June from 1998 to 2004. Each line type and symbol represents estimated mean growth and actual tree growth for each year. Dots connected with grey lines represent same tree. The estimated parameters are shown in Table 3.

to the temperature of the previous year, a positive response was observed in the case of *Q. crispula* and *M. obovata* and a negative response in the case of *A. mono*, *A. amoenum*, *O. japonica*, and *C. cordata*. The sensitivity of *A. amoenum* and *C. cordata* tended to intersect with those of other species in the response to each weather filter other than the temperature of the previous year.

4. Discussion

Our growth model successfully demonstrated the yearly changes in diameter growth in June in response to the weather conditions. This suggests that the tree species in this study significantly respond to the variation in weather conditions. Weather conditions in the summer of previous year and the June of current year both affected the diameter growth in June (Table 3). The significant effect of weather conditions in the previous year on the diameter growth indicated that the trees in this study exhibited a delayed growth response to weather conditions and this was most likely due to the storage of photosynthates. Storage plays an important role in the case of trees with a comparatively long life span and this enables the trees to mitigate the effects of temporal variability in environmental conditions (Chapin et al., 1990). In contrast, weather conditions in June of the current year can affect diameter growth more directly via metabolites. Our result that growth sensitivity to temperature was greater in the current year than in the previous year (Fig. 6) suggests that the effects of weather in the current year on tree diameter growth were stronger than those in the previous year.

The estimated parameters of weather filters reflected the observed weather conditions (Fig. 2, Table 2). The optimum temperature in the summer of previous year for the diameter

growth was almost consistent with the average temperature during that period, and the optimum precipitation in the June of current year was between the average and median of the observed precipitation. The remaining weather filters (temperature in the previous year, PPFD, and VPD) exhibited slopes that intersected the average of each weather factor. These results imply that changes in weather conditions can alter the diameter growth of trees. The optimum values in weather filters close to the average of the observed weather conditions suggests that the trees can adjust their growth to the local weather conditions. The warmer index of our study site (54.1 during observation) is neither the northern nor southern limit for the diameter growth of *A. mono* in Hokkaido Island (Umeki, 2001). In addition, precipitation at our study site is considerably higher in summer (182 mm month^{-1}) compared to that in other related studies (e.g., 107 mm month^{-1}, Hanson et al., 2001; and 655 mm year^{-1} with a summer drought, Ogaya and Penuelas, 2007), suggesting that precipitation is less likely to be a limiting factor for diameter growth in our study. In contrast, Hikosaka et al. (2007) simulated the temperature-dependence of the photosynthetic rate in canopy leaves of *Q. crispula* in TOEF and showed that the optimal leaf temperatures for photosynthesis range from approximately 25 to 30 °C from June to September that are higher than those in our results. This disparity in the optimal temperature can be partly explained by the differences between leaf temperature in the forest canopy and air temperature near the forest floor (1 m aboveground in our study). Since there are few studies that showed the actual responses to weather factors in the case of the studied species, more information would be needed to valid the estimates of weather filters in our study.

Weather indices, W^C and W^P that are affected both by the weather filters and weather conditions had contrasting annual
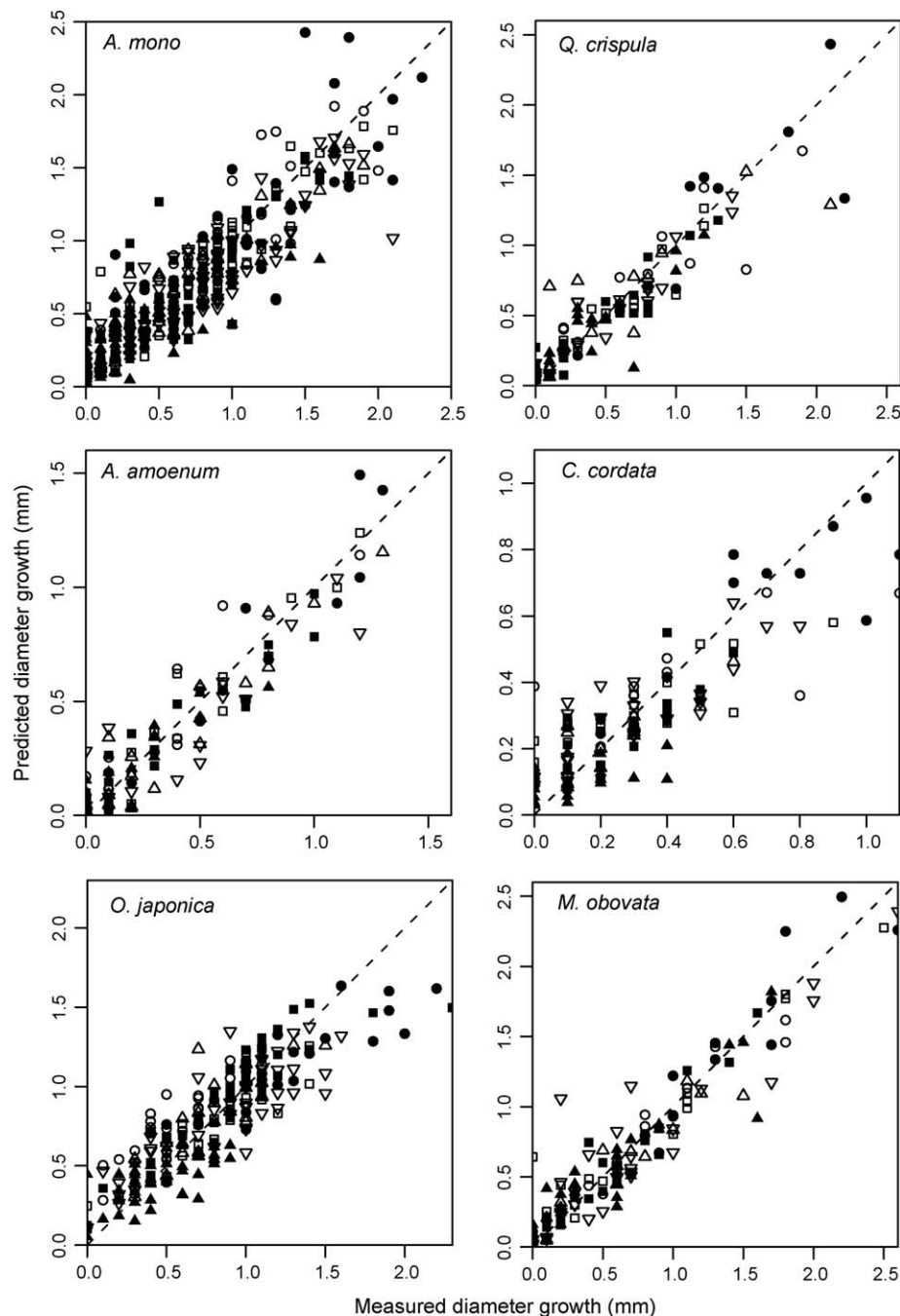
Fig. 5. Relationships between measured and predicted diameter growth for each tree. Symbols are as in Fig. 4.

patterns (Fig. 3). The higher W^C in 1999, for example, was possibly caused by the higher temperature in June 1999 (Table 2), considering the fact that the weather filter of temperature in the current year is monotonically increasing (Fig. 2d). In contrast, W^P tended to be more stable. This may be due to various forms of weather filters in the previous year, convex upward, monotonically increasing and decreasing curve (Fig. 2a–c). Accordingly, these contrasting patterns in W^C and W^P would contribute to describe the annual patterns of diameter growth (Fig. 1).

The estimated parameters of growth models and weather filters were both different among species (Table 3). As a result, these growth models were better overall than the model that ignores species as shown in the AICs of these models. The variation in weather filters represents the differences in the growth

responses to each weather factor among the species. For example, the optimal temperature in the summer of the previous year is higher in Q. crispula and M. obovata than in the other species and the central parameter in June of the current year is also higher in these species. These results suggest that higher temperature favored the growth of Q. crispula and M. obovata compared to that of the other species.

As for the growth model, the size dependency of diameter growth was different among species (Table 3, Fig. 4). Thomas (1996) indicated that diameter growth was greater in the case of tall-statured species in a Malaysian tropical rain forest. Kohyama et al. (2003) demonstrated that the initial growth rate is independent of the maximum height, but the degree of growth reduction is larger in species with smaller maximum sizes than in
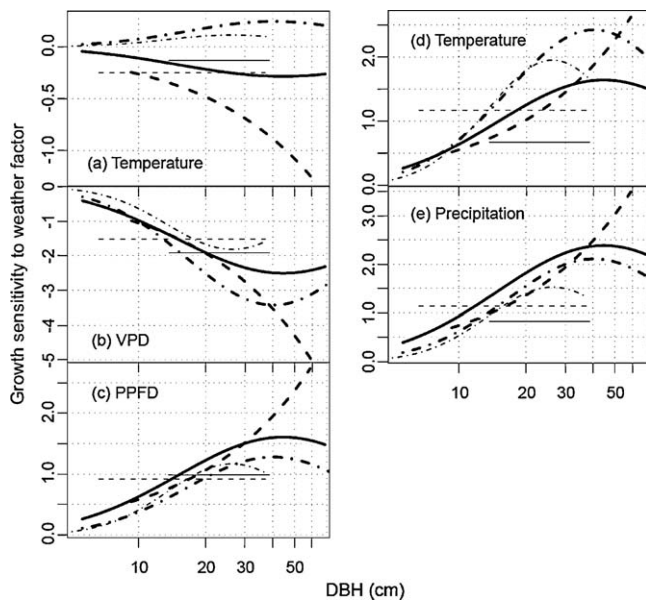
Fig. 6. Results of sensitivity analysis for weather factors in previous and current years: (a) temperature in previous year (T_P); (b) vapour pressure deficit (V); (c) photosynthetic photon flux density (F); (d) temperature in current year (T_C); and (e) precipitation (P). Mean growth responses of each species are represented against tree size (diameter at breast height). Lines are as in Fig. 1.

species with larger maximum sizes. Our study also suggests that the maximum size of the species affected the size-dependency of diameter growth. Canopy species *A. mono*, *O. japonica*, and *Q. crispula* have a greater maximum height (Table 1) and show size-dependent increases in diameter growth, with some growth deceleration in the case of *A. mono* and *Q. crispula*. On the other hand, the shorter species *A. amoenum* and *C. cordata* do not show any size dependent diameter growth. Although *M. obovata* is a shorter species, its diameter growth was found to increase with tree size. Thomas (1996) and Thomas and Bazzaz (1999) reported that growth differences associated with asymptotic height were remarkable in a closed forest; this was due to the "sun-shade tradeoff" along with the light gradient in the vertical profile of the forest. While the other species are mid- to late-successional species (Koike, 1988), *M. obovata* is a gap-phase species known to exhibit a good response to the light environment in canopy gaps (Abe et al., 2002). Additionally, the growth deceleration of *M. obovata* set in when the trees were of a smaller size than in the case of *Q. crispula* and *A. mono*. Therefore, the size-dependent growth of *M. obovata* may be attributed to the life historical traits of gap-phase species while the size-dependency of diameter growth in the other species may depend on the maximum height of the species.

Competition status or light environment for each tree is important factor for tree growth (Uraguchi and Kubo, 2005; Weiskittel et al., 2007; Laubhann et al., 2009). Although we preliminary tested the effects of competition status as a fixed effect, which is basal area of larger trees in same and adjacent grids of one tree, it was not included in the model. Instead, our growth model involve individual variability as a random effect which represents unobserved factors affecting growth rate, such as tree age, genotype, local topography, and light environment. Random effect is useful in the modelling of tree growth to reduce the effect of autocorrelation in the data because of repeated measurement for each tree (Clark et al., 2007; Weiskittel et al., 2007; Laubhann et al., 2009). Tree size, another fixed effect, can partly express light environment or competition status for each tree within a closed forest stand. Since our study site was mature

forest stand with some canopy gaps (Hiura et al., 1998), tree size and individual variability, random effect, together might explain the effect of light environment or competition status on tree growth.

Our results showed that the responses of tree diameter growth to weather conditions were not affected by tree size. Although the growth responses to weather conditions in the case of *Q. crispula*, *O. japonica*, *A. mono*, and *M. obovata* were higher in taller trees than in shorter trees, this was not due to the interactive effect between tree size and weather conditions but due to the assumption of tree diameter growth as a log-linear function of tree size (i.e., the logarithm of DBH) and weather conditions (Eq. (5)). We used a log-linear function for diameter growth because it is the canonical link function for the Poisson family, and this assumption would be appropriate ecologically. Since the components that we assumed to affect diameter growth (i.e., the cells in stems or the leaves of a whole tree) increase exponentially as the tree size increases, the metabolites in stems and the photosynthetic productivity of a whole tree are likely to increase with tree size. It would follow that the response of diameter growth to weather conditions also increase as the tree size increases if the increased metabolites and photosynthetic products increase the diameter growth with tree size. With these assumptions as background, we had expected that the response of diameter growth to weather conditions significantly increase or decrease with tree size over the extent of the assumption due to size-related effect such as hydraulic limitation (Hubbard et al., 1999). However, this effect was not detectable within the period of observation.

The size dependency of diameter growth, instead, caused the interactive effects between tree size and species on the growth responses to weather conditions. For example, above a DBH of 20 cm, growth sensitivity to vapour pressure deficit was higher in the case of *A. mono*, *Q. crispula*, and *O. japonica* rather than in the case of *A. amoenum* and *C. cordata*, while this tendency was reversed in the case of smaller DBH trees (Fig. 6b). The same trend is true for the sensitivity to photosynthetic photon flux density, precipitation, and temperature in the current year (Fig. 7c–e). Such interactive effects between tree size and species on growth responses make it difficult to predict the growth of a mature tree community with various tree sizes under change in weather conditions compared to that of only seedlings. Some studies reported that the physiology or growth responses to weather conditions are ontogenetically different. For example, Cavender-Bares and Bazzaz (2000) showed that physiological responses to drought change with ontogeny in *Quercus rubra*. We additionally suggest that species-specific ontogeny of growth would be required to understand the growth responses to weather conditions of a mature tree community.

The sensitivity analysis also revealed that the slight increase in temperature in the previous years enhances diameter growth in *Q. crispula* and *M. obovata* but depresses those in the other species (Fig. 6a). This indicates that the responses of tree diameter growth may differ among species. Therefore, whenever we assess the effect of future climate change on the growth of a natural forest stand, species-specific growth response to weather conditions would be necessary to avoid over- or under-estimation of the forest growth.

5. Conclusion

We showed that variations within a mature forest, such as tree size and tree species, can independently or interactively affect the growth response of trees to weather conditions. The relationship between the observations and the estimates (Fig. 5)

confirm the validity of our assumptions of growth model, including delayed or nonlinear growth response to weather factors. Although we studied the growth limited in the month of June because the diameter growth mainly occurs in this month that are highly correlated to the annual growth in our study site, some other studies suggest that the mechanisms by which the weather affects diameter growth are different in the early and late growing season in some coniferous trees (Miina, 2000; Yasue et al., 2000). Further investigation would be required to reveal whether and how the seasonal changes in growth affect the variation in annual growth.

The new sensitivity analysis developed in the present study allows us to answer the following two questions with regard to tree growth in a mature forest under changes in weather conditions. First, whether the growth sensitivity of tree species to weather conditions depends on the tree size, and second, whether the increases or decreases in tree-diameter growth with changing climate is species dependent. These findings imply that the changes in forest productivity with changing climate will depend on both the composition of the tree species and the size structure.

Locally, the temporal variation of climatic condition is common to all organisms in a community, yet there are variations in the growth response of trees to change in weather as shown in this study. These variations should be properly assessed and not ignored because the direction of climate change is always uncertain. Various growth responses of trees to weather conditions as shown in this study might alleviate the effects of future climate change on the forest ecosystem function.

Acknowledgements

Appendix A. Generalized linear mixed model

In this appendix, we will derive a likelihood equation to estimate a DBH growth model of trees based on generalized linear mixed model (GLMM, Crawley, 2005). As defined in body, the June growth of tree i in year y is followed to the Poisson distribution with intensity (or mean growth rate for $\{i, y\}$), $\lambda_{i,y}$, which is multiplied by the individual-specific factor, random effects, denoted by r_i. Let **Y** be the set of observation years (**Y** = $\{y\}$ = $\{1998, 1999, \ldots, 2004\}$) and $G_{i,y}$ is the growth of tree individual i and year y. The likelihood of DBH growth for tree i is the convolution of random effects (r_i) and the fixed effects, that is,

$$L_i = \int_0^\infty R(r_i|s) \prod_{y \in Y} f(G_{i,y}|r_i \lambda_{i,y}) dr_i,$$

where $R(r_i|s)$ is the probabilistic density distribution of r_i with mean one and variance parameter s; $f(\ldots)$ is the Poisson distribution as,

$$f(G_{i,y}|\lambda_{i,y}) = \frac{\lambda_{i,y}^{G_{i,y}} \exp(-\lambda_{i,y})}{G_{i,y}!},$$

We choose the Gamma distribution for $R(r_i|s)$, that is,

$$R(r_i|s) = \frac{r_i^{1/s-1} \exp(-r_i/s)}{s^{1/s} \Gamma(1/s)},$$

because this is the natural conjugate prior distribution for the Poisson distribution (Gelman et al., 2004). As the likelihood all over the trees, **T**, is the product of L_i,

$$L(a_0, \ldots, a_6, s) = \prod_{i \in T} L_i(a_0, \ldots, a_6, s),$$

the maximum likelihood estimates for the parameters $\{a_0, \ldots, a_6, s\}$ are obtained by maximizing it.

Appendix B. Parameter estimation and model selection

The parameter estimates for the fixed effects ($\{a_0, \ldots, a_6, s\}$), random effects (s) and weather filters are evaluated by the maximum of the likelihood of the GLMM defined in Appendix A for each tree species. As it is difficult to simultaneously obtain all the estimates, here we carry out a kind of sequential estimation and model selection (in terms of Akaike's information criterion).

In the first step of the sequential model selection, we choose the most appropriate combination of weather filters which generate weather indices to express the yearly change of DBH growth for each tree species shown in Fig. 2.

As it is impossible to seek the best estimate in actual number for all weather parameters, we prepare some discrete values as the candidates for the parameters of weather filters, $a_{tp1} \in \{16.0, 16.4, 16.8, 17.2\}$, $a_{tp2} \in \{4.0, 4.6, 5.2, 5.8\}$, $a_f \in \{0.02, 0.03, 0.04, 0.05\}$, $a_v \in \{0.05, 0.08, 0.11, 0.14\}$, $a_{tc1} \in \{14.2, 14.8, 15.4, 16.0\}$, $a_{tc2} \in \{0.5, 1.0, 1.5, 2.0\}$, $a_{r1} \in \{0.5, 0.7, 0.9, 1.1\}$. The time parameter for rain, a_{r2}, is different from others in that it is common for all species. By setting the candidates for a_{r2} are in $\{0.05, 0.06, 0.07, 0.08, 0.09, 0.10\}$, we choose its estimate such that it minimizes the total AIC for all species after the following procedures for all species are finished.

The coefficients of constant term (a_0) and weather indices (a_3 and a_5) are estimated in the first step where the weather filters are chosen simultaneously. The estimation-selection procedure includes two parts: the ranking by maximized log likelihood without random effects (i.e., generalized linear model, GLM) and "weather filter tournament" by GLMM. First, we generate all possible combinations (16,384) of the candidates for weather filters under a fixed a_{r2}. The maximized likelihoods are evaluated for all the combinations with the GLM version of DBH growth in which the random effects are excluded. In the next step, the "tournament" is carried out to seek the combination of weather filters which maximize the likelihood of GLMM of DBH growth. The best set is sequentially searched in the order of higher fitting in the previous step of GLM likelihood evaluation. The best set is approved by "winning" the subsequent ten sets of weather filters. The estimates for both a_3 and a_5 are restricted to positive values.

By using the best set of weather filters selected above, we evaluate the estimates for the size terms, a_1 and a_2, in GLMM of DBH growth for each species with the model selection by AIC. The preliminary version of the DBH growth model included the effect of suppression by neighboring trees such as one-sided competition (Kohyama, 1991). The intensity of suppression of tree i is defined by the cumulative basal area of neighboring trees larger than tree i. In the model selection procedure by AIC, however, the model including the neighbor suppression term is never selected for all combinations of parameters and weather filters. Therefore, we took off the effect of suppression by neighboring trees as a part of random effect (r_i) in the growth model and does not use in the analysis of this study. Note that all the estimates for a_1, a_3 and a_5 are reevaluated in the step, although they are once estimated in the previous step. Finally, the coefficients

for interaction terms, a_4 and a_6, are estimated for all species, if the size term is selected in the previous procedure.

References

Abe, M., Izaki, J., Miguchi, H., Masaki, T., Makita, A., Nakashizuka, T., 2002. The effects of *Sasa* and canopy gap formation on tree regeneration in an old beech forest. J. Veg. Sci. 13, 565–574.

Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, B.N., Csaki, F. (Eds.), Second International Symposium on Information Theory. Akademiai Kiado, Budapest, pp. 267–281.

Berninger, F., Hari, P., Nikinmaa, E., Lindholm, M., Meriläinen, J., 2004. Use of modeled photosynthesis and decomposition to describe tree growth at the northern tree line. Tree Physiol. 24, 193–204.

Bloom, A.J., Chapin, F.S., Mooney, H.A., 1985. Resource limitation in plants—an economic analogy. Annu. Rev. Ecol. Syst. 16, 363–392.

Bond, B.J., Czarnomski, N.M., Cooper, C., Day, M.E., Greenwood, M.S., 2007. Developmental decline in height growth in Douglas-fir. Tree Physiol. 27, 441–453.

Briffa, K.R., Shishov, V.V., Melvin, T.M., Vaganov, E.A., Grudd, H., Hantemirov, R.M., Eronen, M., Naurzbaev, M.M., 2008. Trends in recent temperature and radial tree growth spanning 2000 years across northwest Eurasia. Phil. Trans. R. Soc. B 363, 2271–2284.

Calama, R., Montero, G., 2004. Interregional nonlinear height-diameter model with random coefficients for stone pine in Spain. Can. J. For. Res. 34, 150–163.

Carrer, M., Urbinati, C., 2004. Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. Ecology 85, 730–740.

Cavender-Bares, J., Bazzaz, F.A., 2000. Changes in drought response strategies with ontogenetic in *Quercus rubra*: implications for scaling from seedlings to mature trees. Oecologia 124, 8–18.

Chapin, F.S., Schulze, E.D., Mooney, H.A., 1990. The ecology and economics of storage in plants. Annu. Rev. Ecol. Syst. 21, 423–447.

Clark, J.S., Wolosin, M., Dietze, M., Ibáñez, I., Ladeau, S., Welsh, M., Kloeppel, B., 2007. Tree growth inference and prediction from diameter censuses and ring width. Ecol. Appl. 17, 1942–1953.

Cook, E.R., Kairiukstis, L.A., 1990. Methods of Dendrochronology. Kluwer Academic Publishers, Dordrecht, 408 pp.

Crawley, M.J., 2005. Statistics: An Introduction Using R. John Wiley & Sons Ltd., West Sussex, UK, 327 pp.

Daniels, L.D., Veblen, T.T., 2004. Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia. Ecology 85, 1284–1296.

Enquist, B.J., 2002. Universal scaling in tree and vascular plant allometry: toward a general quantitative theory linking plant form and function from cells to ecosystems. Tree Physiol. 22, 1045–1064.

Fritts, H.C., 1976. Tree Rings and Climate. Academic Press, New York, NY, 579 pp.

Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2004. Bayesian Data Analysis, second edition. CRC Press, London, UK, 696 pp.

Gough, C.M., Vogel, C.S., Schmid, H.P., Su, H.-B., Curtis, P.S., 2008. Multi-year convergence of biometric and meteorological estimates of forest carbon storage. Agric. For. Metol. 148, 158–170.

Hanson, P.J., Todd, D.E., Amthor, J.S., 2001. A six-year study of sapling and large-tree growth and mortality responses to natural and induced variability in precipitation and throughfall. Tree Physiol. 21, 345–358.

Helle, G., Schleser, G.H., 2004. Beyond CO_2-fixation by Rubisco—an interpretation of C-13/C-12 variations in tree rings from novel intra-seasonal studies on broad-leaf trees. Plant Cell Environ. 27, 367–380.

Hikosaka, K., 1997. Modelling optimal temperature acclimation of the photosynthetic apparatus in C-3 plants with respect to nitrogen use. Ann. Bot. 80, 721–730.

Hikosaka, K., Nabeshima, E., Hiura, T., 2007. Seasonal changes in the temperature response of photosynthesis in canopy leaves of *Quercus crispula* in a cool-temperate forest. Tree Physiol. 27, 1035–1041.

Hiura, T., 2005. Estimation of aboveground biomass and net biomass increment in a cool temperate forest on a landscape scale. Ecol. Res. 20, 271–277.

Hiura, T., Fujito, E., Ishii, T., Naniwa, A., Sugata, S., Ishida, K., Murakami, M., Kato, E., Maeno, H., Fukushima, Y., Sakai, T., 1998. Stand structure of deciduous broad-leaved forest in Tomakomai Experimantal Forest, based on large-plot data. Res. Bull. Hokkaido Univ. For. 55, 1–10.

Hogg, E.H., Wein, R.W., 2005. Impacts of drought on forest growth and regeneration following fire in southwestern Yukon, Canada. Can. J. For. Res. 35, 2141–2150.

Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Winden, P.J., Xiaosu, D., 2001. Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) Cambridge University Press, Cambridge, 944 pp.

Hubbard, R.M., Bond, B.J., Ryan, M.G., 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. Tree Physiol. 19, 165–172.

Imagawa, H., Ishida, S., 1970. Study on the wood formation in trees. Report 1; Seasonal development of the xylem ring of Japanese larch stem, *Larix leptolepsis* GORDON. Res. Bull. Hokkaido Univ. For. 27, 373–394.

Ishida, A., Nakano, T., Matsumoto, Y., Sakoda, M., Ang, L.H., 1999. Diuranal changes in leaf gas exchange and chlorophyll fluorescence in tropical tree species with contrasting light requirements. Ecol. Res. 14, 77–88.

Ishizuka, M., 1981. Seasonal patterns of crown form and diameter growth in *Tilia japonica*. In: Proceedings of Forestry Society of Japan, vol. 29. Hokkaido Branch, (in Japanese), pp. 80–82.

Jones, H.G., 1992. Plants and Microclimate. Cambridge University Press, New York, NY, 452 pp.

Kienholz, R., 1934. Leader, needle, cambial and root growth of certain conifers and their interrelations. Botanical Gazette 96, 73–92.

Kohyama, T., 1991. Simulating stationary size distribution of trees in rain-forests. Ann. Bot. 68, 173–180.

Kohyama, T., Suzuki, E., Partomihardjo, T., Yamada, T., Kubo, T., 2003. Tree species differentiation in growth, recruitment and allometry in relation to maximum height in a Bornean mixed dipterocarp forest. J. Ecol. 91, 797–806.

Koike, T., 1988. Leaf structure and photosynthetic performance as related to the forest succession of deciduous broad-leaved trees. Pl. Sp. Biol. 3, 77–87.

Korzukhin, M.D., Ter-Mikaelian, M.T., Wagner, R.G., 1996. Process versus empirical models: which approach for forest ecosystem management? Can. J. For. Res. 26, 879–887.

Lambers, H., Chapin, F.S., Pons, T.L., 1998. Plant Physiological Ecology. Springer-Verlag, New York, NY, 540 pp.

Laubhann, D., Sterba, H., Reinds, G.J., De Vries, W., 2009. The impact of atmospheric deposition and climate on forest growth in European monitoring plots: an individual tree growth model. For. Ecol. Manage. 258, 1751–1761.

Liming, F.G., 1957. Home made dendrometers. J. For. 55, 575–577.

Matala, J., Hynynen, J., Miina, J., Ojansuu, R., Peltola, H., Sievänen, R., Väisänen, H., Kellomäki, S., 2003. Comparison of a physiological model and a statistical model for prediction of growth and yield in boreal forests. Ecol. Model. 161, 95–116.

Matsuzaki, J., Norisada, M., Kodaira, J., Suzuki, M., Tange, T., 2005. Shoots grafted into the upper crowns of tall Japanese cedar (*Cryptomeria japonica* D. Don) show foliar gas exchange characteristics similar to those of intact shoots. Trees-Struct. Funct. 19, 198–203.

McDowell, N.G., Licata, J., Bond, B.J., 2005. Environmental sensitivity of gas exchange in different-sized trees. Oecologia 145, 9–20.

McLaughlin, S.B., Nosal, M., Wullschleger, S.D., Sun, G., 2007. Interactive effects of ozone and climate on tree growth and water use in a southern Appalachian forest in the USA. New Phytol. 174, 109–124.

Mencuccini, M., Martinez-Vilalta, J., Vanderklein, D., Hamid, H.A., Korakaki, E., Lee, S., Michiels, B., 2005. Size-mediated ageing reduces vigour in trees. Ecol. Lett. 8, 1183–1190.

Midgley, J.J., 2003. Is bigger better in plants? The hydraulic costs of increasing size in trees. Trends Ecol. Evol. 18, 5–6.

Miina, J., 2000. Dependence of tree-ring, earlywood and latewood indices of Scots pine and Norway spruce on climatic factors in eastern Finland. Ecol. Model. 132, 259–273.

Nabeshima, E., 2005. The size dependence of deciduous broad-leaved trees: physiological functions and diameter growth responses to climate variation. PhD Thesis. Hokkaido University, Japan, 87 pp.

Nabeshima, E., Hiura, T., 2007. Size-dependency in hydraulic and photosynthetic properties of three *Acer* species having different maximum sizes. Ecol. Res. 23, 281–288.

Ogaya, R., Penuelas, J., 2007. Tree growth, mortality and above-ground biomass accumulation in a holm oak forest under a five-year experimental field drought. Plant Ecol. 189, 291–299.

Ohtsuka, T., Saigusa, N., Koizumi, H., 2009. On linking multiyear biometric measurements of tree growth with eddy covariance-based net ecosystem production. Glob. Change Biol. 15, 1015–1024.

Rigling, A., Braker, O., Schneiter, G., Schweingruber, F., 2002. Intra-annual tree-ring parameters indicating differences in drought stress of *Pinus sylvestris* forests within the Erico-Pinion in the Valais (Switzerland). Plant Ecol. 163, 105–121.

Ryan, M.G., Yoder, B.J., 1997. Hydraulic limits to tree height and tree growth. Bioscience 47, 235–242.

Saurer, M., Siegwolf, R.T.W., Schweingruber, F.H., 2004. Carbon isotope discrimination indicates improving water-use efficiency of trees in northern Eurasia over the last 100 years. Global Change Biol. 10, 2109–2120.

Shibata, H., Kirikae, M., Tanaka, Y., Sakuma, T., Hatano, R., 1998. Proton budgets of forest ecosystems on volcanogenous regosols in Hokkaido, northern Japan. Water Air Soil Pollut. 105, 63–72.

St. George, S., Meko, D.M., Evans, M.N., 2008. Regional tree growth and inferred summer climate in the Winnipeg River basin, Canada, since AD 1783. Quat. Res. 70, 158–172.

Tabuchi, R., Takahashi, K., 1998. The development of a new dendrometer and its application to deciduous broadleaf tree species in Hokkaido, northern Japan. J. Sust. For. 6, 23–34.

Takahashi, K., Azuma, H., Yasue, K., 2003. Effects of climate on the radial growth of tree species in the upper and lower distribution limits of an altitudinal ecotone on Mount Norikura, central Japan. Ecol. Res. 18, 549–558.

Tenhunen, J.D., Lange, O.L., Harley, P.C., Beyschlag, W., Meyer, A., 1985. Limitations due to water stress on leaf net photosynthesis of *Quercus cossifera* in the Portuguese evergreen scrub. Oecologia 67, 23–30.

Thomas, S.C., 1996. Asymptotic height as a predictor of growth and allometric characteristics Malaysian rain forest trees. Am. J. Bot. 83, 556–566.

Thomas, S.C., Bazzaz, F.A., 1999. Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. Ecology 80, 1607–1622.

Umeki, K., 2001. Growth characteristics of six tree species on Hokkaido Island, northern Japan. Ecol. Res. 16, 435–450.

Uraguchi, A., Kubo, T., 2005. Responses to light in individual growth and reproduction of two *Acer* species and the long-term consequences. Ecol. Res. 20, 177–187.

Weiskittel, A.R., Garber, S.M., Johnson, G.P., Maguire, D.A., Monserud, R.A., 2007. Annualized diameter and height growth equations for Pacific Northwest plantation-grown Douglas-fir, western hemlock, and red alder. For. Ecol. Manage. 250, 266–278.

Yasue, K., Funada, R., Kondo, T., Kobayashi, O., Fukazawa, K., 1996. The effect of climatic factors on the radial growth of Japanese ash in northern Hokkaido, Japan. Can. J. For. Res. 26, 2052–2055.

Yasue, K., Funada, R., Kobayashi, O., Ohtani, J., 2000. The effects of tracheid dimensions on variations in maximum density of *Picea glehnii* and relationships to climatic factors. Trees 14, 223–229.

Yeh, H.Y., Wensel, L.C., 2000. The relationship between tree diameter growth and climate for coniferous species in northern California. Can. J. For. Res. 30, 1463–1471.

Zhao, D., Wilson, M., Borders, B.E., 2005. Modeling response curves and testing treatment effects in repeated measures experiments: a multilevel nonlineear mixed-effects model approach. Can. J. For. Res. 35, 122–132.