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**Dynamics of different branching units in crowns of
Sakhalin spruce,
Picea glehnii (F. Schmidt) Mast.**

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Doctoral Dissertation

Graduate School of Environmental Science

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Summary

Growth and death of branches largely determine the development of crown architecture, which in turn strongly affects not only growth and survival of trees, but also the structure, dynamics, and productivity of forest stands. Therefore, it is crucial to identify the factors controlling branch growth and death within tree crowns to construct reliable models for predicting the growth and development of trees as well as for providing useful guidance for forest management. Because of mutual-shading from neighboring individuals or self-shading within a tree crown, light intensity is commonly heterogeneous within a tree crown in a natural stand. Although light is known as an important factor affecting crown formation and development of various tree species, the role of light in the growth and survival of branches, especially at different levels of branching units, within a tree crown is still poorly understood.

In this study, I investigated the effects of light intensity and other morphological factors on the growth and death of branches and the growth of epicormic shoots in trees of a plantation of *Picea glehnii* (F. Schmidt) Mast. (Sakhalin spruce) in the Sapporo Experimental Forest of Hokkaido University, Sapporo, Hokkaido, Japan. In this study the branches forking from the main trunk were defined as primary branches, and those branching from a primary branch as secondary branches. An epicormic shoot is a shoot initiated from a bud that had been dormant underneath the bark of a branch. Local light intensity was represented by relative photosynthetic photon flux density (rPPFD) recorded above a branch. Trees were categorized into sunlit trees and shaded trees according to their rPPFD above the treetop.

Results showed that, as expected, local light intensity had a significantly positive effect on the number of current-year shoots (shoot number) and length of current-year shoots (shoot length) of both primary and secondary branches in the entire crown. However, the effects of rPPFD exhibited several differences between primary branches and secondary branches, and between sunlit trees and shaded trees. For the primary branches, the difference between shaded and sunlit trees of shoot number and mean shoot length was not significant. However, at the distal part of a primary branch, secondary branches on shaded trees produced significantly more current-year shoots than those on sunlit trees when branches under similar light levels were compared. However, shoot number increased more sharply on sunlit trees than on shaded trees as rPPFD increased.

Furthermore, local light intensity also had a significant effect on the probability of death of both primary and secondary branches. However, the relative influences of its effect on the growth and death of branches were different between these two branching units. In primary branches, shoot number and shoot length were mainly affected by local light intensity, whereas the probability of death of a primary branch was equally affected by both local light condition and the primary branch position within a crown (i.e., the length between basal location of a primary branch and the crown base). A similar result was obtained by another field measurement in which primary branches in a lower part of the crown under a low range of rPPFD (< 3%) were investigated; in this range of rPPFD, the probability of producing one or more current-year shoots on a primary branch was significantly affected by local light intensity. However, the probability of death of primary branch was significantly affected by branch position, while the effect of local light intensity on branch death was not significant.

In contrast to primary branches, the relative influence of local light intensity on shoot production, shoot length and the death of secondary branches all exceeded 65%, indicating that both the growth and survival of a secondary branch mainly depended on its own photosynthetic capability.

In addition, local light intensity had no significant effect on the number of current-year epicormic shoots on primary branches. Primary branches on shaded trees produced more current-year epicormic shoots than those on sunlit trees. Therefore, the production of epicormic shoots occurs in Sakhalin spruce as a normal and an integral part of crown architectural development, and is likely to be a component of a strategy that prolongs tree longevity, especially for those less vigorous Sakhalin spruce trees.

In conclusion, this study revealed that (i) local light intensity alone cannot fully explain the growth and survival of branches, (ii) growth of branches may be inhibited when other branches are under a stronger light intensity within the same crown, (iii) the role of light in the growth and survival varies between different levels of branching units, and (iv) growth of epicormic shoots is likely to be an adaptive growth strategy in the development of crown architecture to maintain crown productivity of Sakhalin spruce.

Chapter 1

General Introduction

The three-dimensional organization of a plant body is defined as the architecture of the plant (Sumida & Komiyama, 1997; Reinhardt & Kuhlemeier, 2002; Sumida *et al.*, 2002). The study of tree architecture emerged as a new scientific discipline in tropic forests approximately 40 years ago (Hallé *et al.*, 1978), which was first used to understand the vegetative growth and structure of tropical trees (Hallé *et al.*, 1978). To date, tree architectural concepts have been an powerful technique to study the phenotypic plasticity of trees (Barthélémy & Caraglio, 2007; Fourcaud *et al.*, 2008; Ishii, 2011; Feng *et al.*, 2012).

Growth and survival of branches within tree crowns largely determine the growth and survival of individual trees (Maillette, 1982; Jerez *et al.*, 2004; Umeki *et al.*, 2006), which in turn influence the structure, dynamics, and productivity of forest stands (Barthélémy & Caraglio, 2007; Feng *et al.*, 2012; Lovynska *et al.*, 2017). Therefore, it is crucial to identify the factors controlling branch growth and death within tree crowns to construct reliable models to predict the growth and development of trees as well as provide useful guidance for forest management (Barthélémy & Caraglio, 2007; Fourcaud *et al.*, 2008).

Tree architecture is constructed not only by endogenous process (e.g., apical dominance) but also by local environment conditions (Barthélémy & Caraglio, 2007; Kawamura, 2010). Because of mutual-shading from neighboring individuals or self-shading within a tree crown, light intensity is commonly heterogeneous within a tree crown in a natural stand (Lacointe *et al.*, 2004; Niinemets, 2007; Gustafsson & Boström, 2013). There is now ample evidence that light is an important factor affecting crown growth and development of various tree species (Williams *et al.*, 1999; Duchesneau *et al.*,

2001; Gratzer *et al.*, 2004). Also, the effects of light intensity in the branch growth and survival has been extensively studied (Takenaka, 2000; He & Dong, 2003; Iio *et al.*, 2009; Sugiura & Tatenno, 2013; Dong *et al.*, 2015). However, the role of light in the growth and survival of branches within a tree crown is still poorly understood.

The concept of branch autonomy with respect to carbon economy has been widely applied to explaining branch growth and death in past decades (Sprugel *et al.*, 1991). It states that, as branches do not import carbon from other branches or organs of its parent tree body except when producing new shoots and reproductive organs, the growth and survival of a branch would be primarily dominated by its local light conditions (Sprugel *et al.*, 1991; Hoch, 2005; Volpe *et al.*, 2008). Meanwhile, several studies using isotopic tracing experiments support this concept of the carbon-autonomous nature of the branch (Lacointe *et al.*, 2004; Hoch, 2005; Volpe *et al.*, 2008).

Trees tend to allocate more resources to branches growing vigorously under the best environments within a crown (Henriksson, 2001; Han & Chiba, 2009; Marty *et al.*, 2009; Millard & Grelet, 2010; Tegeder & Masclaux-Daubresse, 2017). In particular, branches under the best light environments are often allotted more nitrogen to maximize carbon gain (Field, 1983; Anten & During, 2011; Hikosaka, 2014). Therefore, competitive exploitation of resources (e.g., nitrogen) between shaded branches and sunlit branches within the same crown is likely to influence crown development (Sprugel, 2002; Kawamura, 2010). Correlative inhibition predicts that the growth and death of a branch could be affected by other branches within the same crown (Stoll & Schmid, 1998; Takenaka, 2000; Umeki *et al.*, 2006; Dong *et al.*, 2015), considering competition for resources among branches (Anten & During, 2011; Hikosaka, 2014). For example,

Sprugel (2002) showed that a shaded branch on a suppressed or fully shaded *Abies amabilis* (Dougl.) Forbes tree grows better than a branch with a similar light intensity on a sunlit tree. This indicates that light intensity alone may not be able to completely explain the growth and survival of branches within a tree crown (Sprugel, 2002; Chen & Sumida, 2017). It is therefore important to discriminate between the relative contributions of local light conditions and other factors, such as potential resource allocation to the growth and survival of branches, for a comprehensive understanding of the development of crown architecture.

Branching structure of a tree crown is considered as a structure constructed through repetitive production of different branching units (Harper, 1981; Takenaka, 2000). Within a tree crown, primary branches is the branches that directly attached to the main trunk; secondary branches are defined as those that directly branch off from a primary branch. Hence, a tree crown consists of many primary branches while a primary branch is composed of secondary branches. Within a tree crown, light heterogeneity not only exists among primary branches but also among secondary branches. The growth (e.g., the number of current-year shoots produced and the shoot length) and the death of both primary and secondary branches are considered to be closely related to crown development. Furthermore, the response of architectural units (e.g., leaves and branches) within a plant to micro-environmental heterogeneity may vary at different organization levels, such as leaf, shoot and branches (Kawamura & Takeda, 2008; Mori *et al.*, 2008; Kawamura, 2010). Therefore, it is important to investigate the effects of light on the growth and survival of branches considering different levels of branching units within tree crowns.

Within a tree crown, epicormic branches, which form from suppressed or dormant buds underneath the bark of trunk or older branches of a tree, have been documented in many species (Bégin & Filion, 1999; Ishii & Ford, 2001; Waters *et al.*, 2010; Meier *et al.*, 2012). Epicormic branches are considered to occur as a responsive strategy to external stimuli, including pruning (Deal *et al.*, 2003; Takiya *et al.*, 2010), wind damage (Cooper-Ellis *et al.*, 1999), fire (Burrows, 2008; Waters *et al.*, 2010), and insect outbreaks (Landsber & Ohmart, 1989; Marsh & Adams, 1995). In particular, many studies have demonstrated that epicormic sprouting occurs after pruning, which contributes to a suddenly increased light (Kerr & Harmer, 2001; Deal *et al.*, 2003; Gordon *et al.*, 2006; Takiya *et al.*, 2010). Other studies demonstrated that epicormic sprouting can also occur as a normal and integral part of crown architectural development without an obvious external stimuli (e.g., defoliation or pruning) (Ishii & Ford, 2001; Ishii & McDowell, 2002; Ishii *et al.*, 2007).

In this thesis, I designed and performed three experiments (Chapters 3-5) to investigate growth and survival patterns of branches within tree crowns in a plantation of *Picea glehnii* (F. Schmidt) Mast. (Sakhalin spruce). The main objectives were to clarify the effects of light intensity and other morphological factors on the growth and death of branches by considering branch positions within a crown, overall crown light status of a tree, and different levels of branching units, as well as growth of epicormic shoots within tree crowns, for a comprehensive understanding of the dynamics of the formation and maintenance of tree architectures in evergreen coniferous crowns. Based on the results obtained, in Chapter 6, I briefly discussed and summarized the role of local light

conditions in the growth and death of different levels of branching units and epicormic shoots in the crowns of Sakhalin spruce.

Chapter 2

Study Species and Study Site

2.1 Study Species

The study species was an evergreen conifer, Sakhalin spruce, *Picea glehnii* (F. Schmidt) Mast., which mainly distributes in Hokkaido Island of Japan (Kojima, 1991; Aizawa et al., 2015). It can survive in many harsh environment conditions, including swamps, infertile serpentine regions, sand hills or volcanic sands (Tatewaki, 1958; Matsuda, 1989). In addition, this species can resist extremely low temperatures in winter (Sakai & Okada, 1971; Kayama *et al.*, 2007). Due to the great adaptability to severe environment conditions, Sakhalin spruce has been one of the most important coniferous species in silviculture in Hokkaido, Japan (Aizawa *et al.*, 2015).

2.2 Study Site

The study site was a plantation of Sakhalin spruce in the Sapporo Experimental Forest of Hokkaido University, Sapporo, Hokkaido, Japan (43°4'10" N, 141°20'10" E, 17 m a.s.l.). The Sakhalin spruce trees in the plantation was planted in 1981. The annual total precipitation and average temperature between 1981 and 2010 were 1107 mm and 8.9 °C (Japan Meteorological Agency), respectively. This stand was flat and surrounded by some tall deciduous broad-leaved trees (~15 m in height). The mean tree height \pm SD was 8.8 \pm 1.8 m and the mean diameter at breast height (DBH) was 10.2 \pm 2.2 cm in 2013. The area of the plot was 600 m² (40 m \times 15 m). Total basal area and tree density were 15.74

$\text{m}^2 \text{ha}^{-1}$ and 1827ha^{-1} , respectively. In addition, a scaffolding ($15 \text{ m} \times 8 \text{ m} \times 10 \text{ m}$) was constructed to support the field measurement in the study site (see Figure 2.1).

Chapter 3

Patterns of Branch Growth and Survival in Lower Crowns

3.1 Introduction

The architectural development of a tree crown is closely related to the demographic process of branches (Maillette, 1982). Because the development of crown architecture strongly affects tree growth and survival (Küppers, 1989; Sumida & Komiyama, 1997; Sumida *et al.*, 2002), it is necessary to comprehensively clarify the major factors controlling branch growth and death. The study of crown development is also important for the study of timber quality, as it is strongly related to stem taper patterns (Sumida *et al.*, 2013). Light commonly falls in heterogeneous patterns within a tree crown in natural forest communities (Niinemets, 2007). Many studies have demonstrated that light heterogeneity within a tree crown significantly affects the growth and development of the component branches (Takenaka, 2000; He & Dong, 2003; Sugiura & Tatenno, 2013; Dong *et al.*, 2015). However, the effects of light heterogeneity on branches and leaves within a tree crown remains unclear. For example, leaves with greater irradiance generally possess a smaller specific leaf area due to the decrease in leaf thickness (Burns, 2004; Yoshimura, 2010), but this hypothesis does not apply in all cases (Marron *et al.*, 2003; Sellin & Kupper, 2006).

The concept of branch autonomy in a carbon economy has been widely applied to explaining branch growth and death (Sprugel *et al.*, 1991). It states that branches are autonomous and do not depend on carbon imported from other branches or other parts of a tree; light conditions in the growing season are considered to be the determining factor for both branch growth and death (Sprugel *et al.*, 1991; Sprugel, 2002). Several studies using isotopic tracing experiments support this concept of the carbon-autonomous nature of the branch (hereafter ‘branch autonomy’) (Lacointe *et al.*, 2004; Hoch, 2005; Volpe *et*

al., 2008). However, Sprugel (2002) reported that a branch on a shaded tree of *Abies amabilis* (Dougl.) Forbes grows better than a branch under similar local light conditions on a sunlit tree. Several other studies have found that the growth and death of a branch could be affected by other branches (Stoll & Schmid, 1998; Takenaka, 2000; Umeki *et al.*, 2006; Dong *et al.*, 2015). These studies did not fully appear to support the branch autonomy because it assumes that the survival of a branch is determined by the carbon budget of the branch itself. In contrast, correlative inhibition predicts that branches within a tree crown mutually affect each other, because competition for resources other than carbon might exist among branches (Novoplansky *et al.*, 1989; Stoll & Schmid, 1998; Takenaka, 2000; Novoplansky, 2003). Thus, to gain a better understanding of the development of tree architecture, taking the relative importance of branch autonomy and correlative inhibition in the process of branch growth and death into account is needed (Rahman *et al.*, 2014).

Trees can be considered as combinations of similar repetitive units (Harper, 1981). In this study, two levels of a branching unit, that is, the primary and secondary branches, were considered. Primary and secondary branches are defined as branches that branch off from the main stem and that branch off from a primary branch, respectively. A tree crown can be viewed as an assemblage of primary branches that include many secondary branches. Within a tree crown, the local light conditions would vary among primary branches, and light would be heterogeneous among secondary branches located at different positions within a primary branch. The growth (e.g., diameter growth, length of current-year shoots, the number of current-year shoots produced) and survival of secondary branches are considered to be closely related to the growth and death of an entire primary branch. Therefore, to comprehensively understand the patterns of branch

growth, it is important to investigate the effects of light heterogeneity on the growth and survival of branches from different levels of branching units.

In this experiment, I investigated growth and survival patterns of both primary and secondary branches in a plantation of *Picea glehnii* (F. Schmidt) Mast. (Sakhalin spruce) in the lower part of crowns. The objectives were to investigate the effects of morphological factors and light conditions on shoot production, shoot extension, and death of primary and secondary branches. Then, I briefly discuss the causes of branch growth and death of primary and secondary branches in relation to the relative importance of branch autonomy and correlative inhibition.

3.2 Methods

3.2.1. Field Measurements

In this study, all the data were obtained using nondestructive measurements. The crown base and the crown base height were defined as the basal location of the lowest live primary branch on a main stem and its height above ground level, respectively. In July 2013, DBH, tree height, and the crown base height were measured for each tree in the study site. These trees were grouped into two DBH classes: 7.0–9.9 cm, and >10.0 cm. Eight trees were selected from each diameter class. Hence, a total of 16 trees were chosen as the sample trees (Table 3.1). Because of partial shading from neighboring broad-leaved trees around the site, five out of the 16 trees at the edge of the study site died during the field measurement period from July 2013 to July 2014 (Table 3.1).

Because light resources were heterogeneous not only among primary branches within a tree crown but also among secondary branches within a primary branch, both types of

branches were selected to investigate the effects of light conditions on branch growth and death. In order to study the growth and death of branches simultaneously, branches in the lower part of a crown were chosen, because branch death mainly occurs in the lower part of the crown rather than in the upper part (Hartman *et al.*, 2000; Ishii & McDowell, 2002; Ishii *et al.*, 2017). Four primary branches were randomly chosen from each sample tree. Therefore, a total of 64 primary branches (16 trees \times 4 branches) were selected. The mean branch diameter at the basal location \pm SD and the mean length of the primary branches in July 2013 were 13.5 ± 4.0 mm and 113.0 ± 33.6 cm, respectively. For all these primary branches, the length between the basal location of a primary branch and the crown base (L_{CB} , cm) was measured to document the primary branch location within a crown.

All of the 64 primary branches were categorized into those having one or more current-year shoots and those that did not in July 2013. For each of the 26 primary branches having one or more current-year shoots, two or three opposite pairs of secondary branches were selected from each of three positions (the distal, middle, and proximal parts) in a primary branch in July 2013. A total of 121 secondary branches were selected. The mean basal diameter and the mean length (\pm SD) of the secondary branches were 4.5 ± 3.3 mm and 38.4 ± 31.9 cm, respectively. The number of all current-year shoots on all of the selected secondary branches was counted. Some of these current-year shoots (five, on average) were randomly chosen from each secondary branch, and their lengths were also measured in July 2013. The mean current-year shoot length of a primary branch was calculated as the mean length for all these secondary branches selected within the primary branch. Because extension of the current-year shoots ceased before the July measurement, this length represents the entire shoot extension growth of 2013. A primary or secondary branch on which all the needle colors changed from green to yellow and finally fell off

by December 2013 was identified as a dead branch. The number of living primary and secondary branches was recorded in each month from July 2013 to July 2014.

3.2.2. Light Measurements

Photosynthetic photon flux density (PPFD; $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) for all 64 primary branches was measured with two quantum sensors (PAR-01L, Prede Co., Ltd., Tokyo, Japan) on overcast days in May 2014. In the study site, there was no anthropogenic damage (e.g., branch pruning) or natural disturbance (e.g., typhoons or fires) from 2013 to 2014. Because I did not measure light intensity in 2013, the relative photosynthetic photon flux densities (rPPFDs) measured in 2014 were used as surrogates of rPPFDs in 2013. When measuring rPPFDs, one sensor was fixed on the top of a vertically standing 15 m long pole, approximately 1 m higher than the top of the canopy in the study site. Another sensor was placed horizontally above the tip of primary or secondary branches and was held there for more than 20 seconds when measuring light intensities above the branches. Measurements from both sensors were recorded simultaneously at an interval of 20 seconds using a data logger (FTJR-2 CH, M.C.S Co., Ltd., Sapporo, Japan). The rPPFD was calculated as the ratio of PPFD above a primary or secondary branch to that above the canopy. This rPPFD measurement was repeated three times for each primary or secondary branch, and their average was defined as the rPPFD of each primary or secondary branch.

As explained below, I analyzed whether the number of current-year shoots, the probability of death, and the mean length of current-year shoots on a secondary branch were affected by its position on a primary branch. Meanwhile, these attributes may also be affected by rPPFD on these secondary branches, but I did not measure rPPFD on

secondary branches during 2013 and 2014. Because the positions of the secondary branches and the rPPFDs on these secondary branches were expected to be closely interrelated, the relationship between the position of secondary branches and their light conditions was also examined as follows. In May 2015, six trees were selected from the 11 sample trees that had survived (see Table 3.1). Then, another 24 primary branches were newly selected from these trees. Using the method described above, two or three pairs of secondary branches were randomly selected from the distal, middle, and proximal parts of each of these primary branches in May 2015. A total of 126 new secondary branches were selected and the rPPFD values of these primary and secondary branches were measured in June 2015. Note that these newly selected branches were used only for examining the relationship between rPPFD of the primary branch in 2015 and L_{CB} , and between rPPFD of the secondary branch in 2015 and secondary branch positions, respectively.

3.2.3. Statistical Analysis

Primary Branches

The effects of L_{CB} (cm) in 2013 and natural-log transformed rPPFD (%) (hereafter ‘ln(rPPFD)’) measured in May 2014 on the probability (P) of shoot production (probability of producing at least one current-year shoot) in the growing season of 2013 were analyzed by generalized linear mixed models (GLMM). The ln(rPPFD) and L_{CB} were set as fixed effects, and individual trees as the random effect. The logit link function was used to transform the binary variable Y into the response variable used in the GLMM,

that is, logit of the probability of shoot production P . The model of GLMMs was formulated as follows:

$$Y_{ij} = \ln\left(\frac{P_{ij}}{1-P_{ij}}\right) = \beta_0 + \beta_1 x_{ij} + I_i \quad , \quad (3.1)$$

where $Y_{ij} = 1$ if a primary branch j on tree i produced at least one current-year shoot and 0 if otherwise; x_{ij} represents the $\ln(\text{rPPFD})$ or L_{CB} for primary branch j on tree i ; β_0 and β_1 are the fixed effects; I_i is the random intercept of tree i .

The effects of L_{CB} (cm) in 2013 and $\ln(\text{rPPFD})$ in May 2014 on the probability of the death of primary branches between 2013 and 2014 were also analyzed with Equation (3.1), where $Y_{ij} = 1$ if a primary branch j on tree i died during the period between July 2013 and July 2014, and 0 if it survived.

The effects of L_{CB} (cm) in 2013 and $\ln(\text{rPPFD})$ above the primary branches in May 2014 on the mean length of current-year shoots per primary branch (cm) in 2013 were analyzed using linear mixed models (LMMs). The mean length was the response variable, $\ln(\text{rPPFD})$ and L_{CB} were the fixed effects of predictor variables, and individual trees was the random effect.

The relationship between L_{CB} (cm) and $\ln(\text{rPPFD})$ above a primary branch was also investigated with LMMs, where data from six trees that were selected in both 2013 and 2015 were separately investigated to determine if the results of the two years were comparable. Although both L_{CB} and $\ln(\text{rPPFD})$ were the predictor variables in the abovementioned GLMMs and LMMs, for convenience, $\ln(\text{rPPFD})$ was regarded as the response variable, and L_{CB} as the fixed effect of the predictor variable, and individual trees as random effect.

Secondary Branches

The effects of the position of secondary branches within a primary branch on the current-year shoot production (the number of current-year shoots produced) in 2013 were analyzed by GLMM. The position of secondary branches (distal, middle, and proximal) was the categorical fixed effects predictor variable and primary branches within an individual tree were set as the random effects. The logarithmic link was assumed for the relationship between the response variable Y and the number of current-year shoots N_s in each secondary branch position. Because the position was a categorical variable, the three positions were coded using dummy variables (Suits, 1957; Draper & Smith, 2014). The model is briefly expressed using Equation (3.2):

$$Y_{ij} = \ln(N_s)_{ij} = \alpha + \beta_1 x_{1ij} + \beta_2 x_{2ij}, \quad (3.2)$$

where $(x_1, x_2) = (0,0)$ for the distal position, $(x_1, x_2) = (1,0)$ for the middle position, and $(x_1, x_2) = (0,1)$ for the proximal position, and β_1 and β_2 are coefficients specific to each position. Because the data of the response variable included many zero data values (i.e., many secondary branches with no current-year shoot production) (Venables & Ripley, 2013), negative binomial distribution was assumed for the response variable (Zeileis *et al.*, 2008). The effects of the position of a secondary branch on the probability of death P of a secondary branch between July 2013 and July 2014 were also analyzed by GLMM. By assuming a binomial distribution, the response variable Y was expressed as the logit link of the probability of death P , where $P = 1$ if a secondary branch died during the period above; otherwise $P = 0$. The positions of secondary branches were coded using dummy variables as in the right side of Equation (3.2). The primary branches within an individual tree were set as a random effect.

Further, the effects of the position of a secondary branch on the mean length of current-year shoots L_s (cm) on secondary branches in 2013 were examined by LMMs. The positions of secondary branches were the categorical response variable. As in Equation (2), it was coded using a dummy variable.

As mentioned above, the relationship between rPPFD and the secondary branch positions was examined. Natural-log transformed rPPFD (%) measured in 2015 was the quantitative response variable, and primary branches within an individual tree were set as the random effects.

Tukey's pairwise comparison method in the multcomp package (Hothorn *et al.*, 2016) of R (R Core Team, 2015) was used for multiple comparisons among secondary branch positions after the analysis of the abovementioned GLMMs. For the analysis concerning branch death, data from the sample trees that died between 2013 and 2014 (Table 3.1) were excluded. The lme4 (Bates *et al.*, 2014) and glmmADMB packages (Bolker *et al.*, 2012) of R version 3.2.2 (R Core Team, 2015) were used to perform the LMMs and GLMMs, respectively.

3.3 Results

3.3.1 Primary Branches

Figure 3.1a shows the relationship between rPPFD above a primary branch and the probability that one or more current-year shoots are produced on a primary branch. The rPPFD had a significant effect ($p = 0.01$) on the probability of producing current-year shoots (Table 3.2, Figure 3.1a). The rPPFDs above the primary branches were about <3%, indicating that the branches that were chosen in the lower part of the crown experienced

dark conditions. Primary branches with more intense light conditions were more likely to produce current-year shoots than those with darker conditions (Figure 3.1a). However, branch position (L_{CB}) had no significant effect ($p = 0.29$) on the current-year shoot production (Table 3.2, Figure 3.1b).

For the primary branches that produced one or more current-year shoots, the effects of rPPFD and L_{CB} on the mean length of current-year shoots L_s were examined. However, both of these effects were not significant ($p = 0.66$, $p = 0.83$; Table 3.2).

In addition, the effects of rPPFD above a primary branch and the effects of L_{CB} on the probability of death of a primary branch were examined. In contrast with the results shown in Figure 3.1, the effect of $\ln(\text{rPPFD})$ was not significant ($p = 0.18$; Table 3.2, Figure 3.2a), but the effect of L_{CB} was significant ($p = 0.04$; Table 3.1, Figure 3.2b). The probability significantly decreased with increasing L_{CB} (Table 3.2, Figure 3.2b). Incidentally, the relationships between L_{CB} and $\ln(\text{rPPFD})$ above primary branches were not significant in both 2013 and 2015 ($p = 0.23$, $p = 0.38$, respectively; Table 3.3).

3.3.2 Secondary Branches

The location of a secondary branch (distal, middle, and proximal parts on a primary branch) had a significant effect on the mean number of current-year shoots per secondary branch (Table 3.4; $p < 0.05$). Secondary branches at the distal part of a primary branch produced more current-year shoots than those at the proximal part (Figure 3.3). However, the difference in the mean length of current-year shoots was not significant among

secondary branches at the distal, middle, and proximal parts of primary branches ($p > 0.05$) (Table 3.4, Figure 3.4).

The effect of the position of secondary branches on the probability of death of a secondary branch between 2013 and 2014 is shown in Table 3.4. The probability of death was significantly higher for the proximal part of these secondary branches than in the distal part ($p < 0.05$, Table 3.4). Incidentally, $\ln(\text{rPPFD})$ above the secondary branches that had been selected in 2015 was stronger on the distal part of a primary branch than on the proximal part (Table 3.5, Figure 3.5). Therefore, it is possible that rPPFD on secondary branches affected the probability of their death.

3.4. Discussion

3.4.1. Primary Branches

Local light conditions above individual primary branches determined the probability of the production of one or more current-year shoots (Table 3.2, Figure 3.1), which is consistent with previous studies (Koike, 1989; Takenaka, 2000; Dong *et al.*, 2015). Primary branches with a lower light intensity were expected to have a higher tendency to die (Sprugel *et al.*, 1991) according to branch autonomy. However, the death of primary branches in the lower part of a crown, where the relative photosynthetic photon flux density (rPPFD) levels were about $<3\%$ (Figure 3.2), was not related to the light conditions of the branch, but was significantly affected by the length between branch basal location and the crown base (L_{CB}) within the tree crown (Table 3.2, Figure 3.2). These results suggest that, under this low rPPFD range, the death of primary branches

was not determined solely by the light intensity. In this sense, the primary branches investigated here could not be regarded as fully autonomous in the crown of Sakhalin spruce.

The reason why the length from the crown base was related to branch death remains unknown, but it might be ascribed to the mechanism that causes correlative inhibition. The Introduction states that the growth conditions of other parts of the crown affect survival of an individual branch. That is, when branches in the upper part of the crown are growing vigorously under sunlit conditions and resources such as nitrogen are limited, the resources stored in the older part of the crown are translocated to the vigorously growing part (Han & Chiba, 2009; Marty *et al.*, 2009; Millard & Grelet, 2010). This is thought to be a reason why lower branches in a sunlit crown are prone to death and cause correlative inhibition (Novoplansky, 2003). In this experiment, I did not measure light conditions or growth/death patterns of primary branches in the upper part of the crown, it remains unclear whether or not the observed branch death in the lower part of the crown resulted from correlative responses to the light conditions in the upper part. However, if the upper, vigorously growing sunlit branches acquire necessary resources that are translocated from the branches at the lowest part of the crown, the lowest branches may easily die because of the loss of these translocated resources. This branch death may occur even if the light conditions of the lower branches were sufficient to produce a positive photosynthetic budget in those lower branches. Trees may translocate resources from the most unnecessary parts, such as the lower branches. This may be a reason why L_{CB} was negatively related to the probability of branch death irrespective of the light conditions (Table 3.2, Figure 3.2). If so, the effect of L_{CB} is a representation of correlative inhibition. Clearly, further studies considering resource translocation are needed to better understand

the relationship between branch death and the length from the crown base in relation to the physiological mechanisms regarding correlative inhibition.

3.4.2. Secondary Branches

In contrast to the results for primary branches, secondary branches exhibited ordinary responses to the ambient light conditions. Within a primary branch, the secondary branches at the proximal part not only produced fewer current-year shoots (Figure 3.3) but also exhibited a higher probability of death than those at the distal part (Table 3.4). In addition, light intensities of secondary branches at the proximal part were lower than those of the distal part (Figure 3.5). Therefore, the death of secondary branches at the proximal part was probably primarily caused by low light conditions (Marty *et al.*, 2009). If continuous death of secondary branches occurs, which moves from the proximal part towards the distal part and results in a decrease in the amount of needles produced per primary branch, this change would reduce the photosynthetic and transpirational activity of the entire primary branch (Nobel *et al.*, 1975; Lambers *et al.*, 2008). Although I did not measure the amounts of needles and current-year shoots per primary branch, the results suggest that a decrease in the amount of needles per primary branch occurs from the proximal to distal part on a primary branch. Considering that such decreases would be pronounced in primary branches of the lower part of the crown, the light independent death of primary branches (Figure 3.2) may be affected by the degree to which the amount of needles per primary branch has decreased.

3.4.3. Branch Autonomy versus Correlative Inhibition

Results suggest that branch autonomy could explain the growth of primary branches in the sense that the probability of current-year shoot production had a significant positive relationship with rPPFD (Figure 3.1). However, light conditions or branch autonomy alone were not likely to explain the death of primary branches (Figure 3.2). In other words, the factor responsible for branch autonomy (local light conditions) can explain both growth (current-year shoot production) and death of secondary branches (Table 3.4), but this factor could not explain the death of primary branches. This suggests that factors affecting current-year shoot production and death of a primary branch may be different from those affecting secondary branches. In addition, the factor responsible for correlative inhibition could be the dominant factor causing the death of an entire primary branch. These findings also suggest that the relative importance of correlative inhibition and branch autonomy in branch growth and death is different for primary and secondary branches.

Despite spatial and temporal variability of the light conditions of branches, the measurement of relative PPFDs on overcast conditions has been accepted as a method to conveniently assess the light conditions of branches (Parent & Messier, 1996; Sumida *et al.*, 1997; Gendron *et al.*, 1998; Comeau *et al.*, 1998; Dewar *et al.*, 2012; Osada *et al.*, 2014). However, the growth and longevity of branches would be influenced by stand density, inter-tree competition (Mäkinen, 2002; Weiskittel *et al.*, 2007; Courbet *et al.*, 2012), plant hormones (Cline, 1994), and programmed cell death (Hoeberichts & Woltering, 2003). Hence, it is desirable for further work to take such physical and physiological factors into consideration to clearly clarify the limiting factors for branch growth and death within the crowns of adult trees in situ.

In this experiment, results showed that factors affecting current-year shoot production on a primary branch and death of an entire primary branch were different in the lower part of tree crown. As expected, the former was related to light conditions. However, the latter was not related to light conditions, which was related to the location of the primary branch measured from the crown base. In contrast to primary branches, both shoot production and death of secondary branches exhibited ordinary responses to the ambient light conditions. This suggests that while local light conditions are relevant to shoot production of primary and secondary branches, death of the primary branch may be related to some morphological attributes concerning the distance to the crown base, and that the relative importance of correlative inhibition and branch autonomy in branch growth and death may be different for primary and secondary branches as well.

Chapter 4

Patterns of Growth and Survival of Different Branching Units

4.1 Introduction

Light condition is an important factor affecting crown growth and development of various tree species (Williams *et al.*, 1999; Duchesneau *et al.*, 2001; Gratzner *et al.*, 2004). Due to mutual-shading from neighboring individuals or self-shading within a tree crown, light intensity is heterogeneous in a natural stand (Lacointe *et al.*, 2004; Niinemets, 2007; Gustafsson & Boström, 2013). To date, effects of light intensity on branch growth and survival have been extensively studied (Takenaka, 2000; Goulet *et al.*, 2000; He & Dong, 2003; Iio *et al.*, 2009; Sugiura & Tateno, 2013; Dong *et al.*, 2015). Typically, the number of current-year shoots produced on a branch is known to increase with increasing light intensity above it (Takenaka, 2000; Chen & Sumida, 2017).

Branching structure of a tree crown is considered as a structure constructed through repetitive production of different branching units (Harper, 1981; Takenaka, 2000). A tree crown consists of many primary branches, that is, the branches that directly attached to the main trunk. Likewise, a primary branch is composed of secondary branches, which are defined as those that directly branch off from a primary branch. Light heterogeneity not only exists among primary branches within a tree crown, but also among secondary branches within a primary branch. The growth (e.g., current-year shoot number and shoot length) and death of both primary and secondary branches are thought to be closely related to crown development. However, existing studies rarely investigated the effects of light heterogeneity on branch growth and death by considering different levels of branching units within the whole crowns of adult trees *in situ*.

As a concept explaining branch growth and death with respect to carbon economy, branch autonomy has become popular in the past decades (Sprugel *et al.*, 1991; Sprugel, 2002). It states that, as branches do not import carbon from other branches or organs within the same tree body except when producing new shoots and reproductive organs (Desalme *et al.*, 2017), the growth and survival of a branch would be primarily dominated by its local light conditions (Sprugel *et al.*, 1991; Hoch, 2005; Volpe *et al.*, 2008).

However, Sprugel (2002) showed that a shaded branch on a suppressed or fully shaded *Abies amabilis* (Dougl.) Forbes tree grows better than a branch with a similar light intensity on a dominant (sunlit) tree. In addition, Chen and Sumida (2017) found that in branches of the lowest part of a crown of *Picea glehnii* (F.Schmidt) Mast. (Sakhalin spruce), death of branches significantly decreased with increasing distance from the crown base, while light environments above the branches did not have significant effects on branch death. These studies suggest that the growth and survival of a branch may not be determined by its local light conditions alone.

Trees tend to allocate more resources (e.g., nitrogen) to branches growing vigorously under the best environments within a crown (Henriksson, 2001; Han & Chiba, 2009; Marty *et al.*, 2009; Millard & Grelet, 2010; Tegeder & Masclaux-Daubresse, 2017). For example, branches under the best light environments within a plant are often allotted by more resources such as nitrogen to maximize photosynthesis (Field, 1983; Hikosaka, 2014). As a consequence, within a tree crown, growth of a branch under relatively darker conditions could be inhibited even if the light level itself is not so low as to cause growth inhibition. This phenomenon is called correlative inhibition (Novoplansky *et al.*, 1989; Stoll & Schmid, 1998; Takenaka, 2000; Dong *et al.*, 2015). In other words, exploitative

competition of resources between shaded branches and sunlit branches within the same crown is likely to influence branch growth (Sprugel, 2002; Kawamura, 2010). Therefore, it is important to estimate relative contributions of local light conditions and correlative inhibition to the growth and survival of branches towards a comprehensive understanding of the development of crown architecture.

In this study, I investigated the effects of local light conditions of branches, locations of branches within a crown or within a branch, and the light conditions above the crowns of sunlit and shaded trees on the growth and survival of branches in a plantation of Sakhalin spruce. Based on the results obtained, I attempted to assess the importance of the factors affecting growth and death of branches in terms of different levels of branching units.

4.2 Methods

4.2.1 Field Measurements

All the data in this study were obtained using nondestructive measurements. The crown base was defined as the basal location of the lowest live primary branch on a main stem. The length between the crown base (L_{CB} , cm; hereafter referred to as the primary branch position) and the base of a primary branch on a main stem was measured to represent its branch position within a crown. Crown length was measured as the length between the crown base and the top of a tree. The crown of each sample tree was divided into two sections with equal depth, the lower half and the upper half, which are hereafter referred to as the lower crown and the upper crown, respectively.

In April 2016, after measuring DBH of all the trees in the study plot, eight trees, ranging from the smallest to the largest in DBH, were selected as the sample trees (Table 4.1). For each tree, 13 to 20 primary branches were selected in the lower and the upper crowns, where the number of branches selected depended on the crown length. In total, I selected 126 primary branches.

The mean branch diameter (\pm SD) at the basal location and the mean length (\pm SD) of the primary branches were 13.4 ± 3.1 mm and 104.8 ± 26.1 cm, respectively. For each primary branch, two or three opposite pairs of secondary branches were selected from each of the three parts: the distal, the middle, and the proximal parts. These three parts are hereafter referred to as the secondary branch position. A total of 739 secondary branches were selected. The mean length (\pm SD) of the secondary branches was 30.3 ± 13.6 cm.

In late July 2016, after the shoot production of current year finished, the total numbers of the current-year shoots were recorded for each primary branch and for the selected secondary branch, respectively, of which several were randomly chosen and their shoot lengths were measured for assessing extension growth at the levels of primary and secondary branches, respectively. Because extension of the current-year shoots ceased before the July measurement, the length of current-year shoots measured represents the entire shoot extension in the growing season. A primary or secondary branch on which the color of all the needles changed from green to yellow and finally fell off by December 2016 was regarded as a dead branch. The number of dead primary and secondary branches was recorded at the end of December 2016.

4.2.2 Light Measurements

Photosynthetic photon flux density (PPFD; $\mu\text{E m}^{-2} \text{s}^{-1}$) was measured for all the 126 primary branches and the 739 secondary branches using two quantum sensors (PAR-01L, Prede Co., Ltd., Tokyo, Japan) on overcast days in September 2016. When measuring rPPFDs, one sensor was fixed on the top of a vertically standing pole 15 m long, approximately 1 m higher than the canopy top at the study site; another sensor was placed horizontally above the tip of a branch and held there for more than 20 seconds. Measurements from both sensors were recorded simultaneously at 20-second intervals using a data logger (FTJR-2 CH, M.C.S Co., Ltd., Sapporo, Japan). The rPPFD was calculated as the ratio of PPFD above a branch to that above the canopy. This rPPFD measurement was repeated three times and their average was defined as the rPPFD of each branch. In October 2016, the rPPFDs right above the treetop of each sample tree were also measured using the same method. Then the sample trees were grouped into the shaded trees (rPPFD < 50%) and the sunlit trees (rPPFD > 50%). Three of the eight sample trees were the sunlit trees (Table 4.1).

4.2.3 Statistical Analysis

Primary branches

In the analysis, the data of rPPFD were natural-log transformed to meet the assumption of normal residuals. The effects of natural-log transformed rPPFD (%) (hereafter ‘ln(rPPFD)’) and the crown light status (shaded or sunlit trees) on the number of current-year shoots on primary branches in the lower and the upper crown were analyzed separately using generalized linear mixed models (GLMMs), where crown light status

and $\ln(\text{rPPFD})$ of primary branches were designated as the fixed effects, and individual trees as the random effect. The global model is expressed as follows:

$$\ln(y_{ij}) = \alpha_0 + \alpha_1 x_{1ij} + \alpha_2 x_{2ij} + \alpha_3 x_{1ij} x_{2ij} + I_i \quad , \quad (4.1)$$

where y_{ij} is the number of current-year shoots produced by primary branch j of tree i , x_{1ij} is the $\ln(\text{rPPFD})$ of a primary branch j of tree i , x_{2ij} is a categorical variable for the crown light status with two levels: the sunlit and shaded, α_0 , α_1 , α_2 and α_3 are coefficients of the fixed effects, and I_i is the random intercept for an individual tree i . Because the data of a response variable, the number of current-year shoots, included many zero data values (i.e., many primary branches with no current-year shoots), negative binomial distribution was assumed for the residuals to deal with overdispersion (Zeileis *et al.*, 2008).

The effects of $\ln(\text{rPPFD})$ and crown light status on current-year shoot length of primary branches were analyzed for the lower and upper crowns independently by using linear mixed models (LMMs). The response variable was the natural-log transformed mean current-year shoot length per primary branch. The fixed and random effects were the same as in Eq. (4.1). The full model is expressed as follows:

$$\ln(y_{ij}) = \beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} + \beta_3 x_{1ij} x_{2ij} + I_i \quad , \quad (4.2)$$

where y_{ij} is the length of current-year shoots of primary branch j of tree i , x_{1ij} is the $\ln(\text{rPPFD})$ of a primary branch j of tree i ; x_{2ij} is a categorical variable representing the crown light status, β_0 , β_1 , β_2 and β_3 are coefficients of the fixed effects, and I_i is the random intercept for tree i .

Because the dead primary branches were only observed in the lower part of crown, the data in the lower and upper crowns were combined together when analyzing the effects of $\ln(\text{rPPFD})$ and crown light status on the probability of primary branch death.

The logit function was used to transform the actual binary variable y_{ij} to the response variable used in the GLMM, that is, the logit of the probability of the death of primary branches π_{ij} . The $\ln(\text{rPPFD})$ and crown light status were set as the fixed effects with the random intercepts indicating individual trees. The full model is formulated as the following equation:

$$y_{ij} = \ln\left(\frac{\pi_{ij}}{1-\pi_{ij}}\right) = \gamma_0 + \gamma_1 x_{1ij} + \gamma_2 x_{2ij} + \gamma_3 x_{1ij} x_{2ij} + I_i, \quad (4.3)$$

where $y_{ij} = 1$ if a primary branch j on tree i died during the period between April 2016 and December 2016, and 0 if it survived, x_{1ij} is the $\ln(\text{rPPFD})$ of a primary branch j of tree i ; x_{2ij} is a categorical variable representing the crown light status, γ_0 , γ_1 , γ_2 and γ_3 are coefficients of the fixed effects, and I_i is the random intercept for tree i .

Moreover, the effects of $\ln(\text{rPPFD})$ and branch position (L_{CB}) on the shoot number, shoot length and probability of primary branch death were also analyzed using Eqs 4.1-4.3. The fixed effects were the $\ln(\text{rPPFD})$ and branch position with the random intercepts among individual trees.

Model selection method based on information criteria is popular in ecological studies, which provides an approach to identify the model that can ‘best’ approximate the data from the set of candidate models (Symonds & Moussalli, 2011; Galipaud *et al.*, 2014). However, whether so-called the ‘best’ model is the best or not often is uncertain when several competing models exist (Symonds & Moussalli, 2011; Galipaud *et al.*, 2014). This was the case when assessing the effects of $\ln(\text{rPPFD})$ and the crown light status (or L_{CB}) on the shoot number, shoot length, and probability of death of primary branches. To deal with the uncertainty of model selection, the model averaging method was adopted in estimating the model parameters of Eqs 4.1-4.3, in which the candidate

models selected by Royall's 1/8 rule for evidence strength (Royall, 1997) was used. In this study, the natural model averaging method (Symonds and Moussalli 2011) was employed, which keeps the averaged estimate of parameters in the original scale. A complete description of the averaging method can be found in Symonds and Moussalli (2011).

Secondary branches

The effects of $\ln(rPPFD)$ and crown light status on the shoot number, shoot length and the probability of death of secondary branches at the distal, the middle and the proximal parts of primary branches were also analyzed using (G)LMMs, followed by the model averaging method (Symonds & Moussalli, 2011). As in Eqs 4.1-4.3, the $\ln(rPPFD)$ and the crown light status were the fixed effects with random intercepts indicating individual trees.

In addition, the differences in $\ln(rPPFD)$, shoot number and shoot length of primary and secondary branches were tested among the lower crown of the shaded trees, the upper crown of the shaded trees, the lower crown of the sunlit trees, and the upper crown of the sunlit trees using two-way ANOVA, followed by Tukey's HSD (honestly significant difference) test.

Relative influence of light intensity, branch position, crown section, and crown light status

I employed the boosted regression trees (BRTs) analysis to quantify the relative influence of $\ln(rPPFD)$, the branch position, the crown section and the crown light status (i.e., the sunlit or the shaded) on shoot number, shoot length and the probability of death for

primary and secondary branches. BRTs can deal with multiple types of variables: continuous, categorical, missing and non-dependent ones (De'Ath, 2007; Elith *et al.*, 2008; Buston & Elith, 2011). BRTs has been widely used in ecological modelling and prediction (Elith *et al.*, 2008). The relative influence of predictor variables in BRTs is calculated based on the number of times that a variable is selected from results of multiple models created by iteration and its improvement to the model as a result of each selection (Friedman & Meulman, 2003). The relative influence of each predictor variable is scaled so that the sum of all model predictor variables adds up to 100%. The learning rate parameter in BRTs controls the overall weight of each model of the individual regression tree (i.e., individual iteration). Considering that model performance is always improved by less learning rate and more number of the trees (the number of iterations) (Ridgeway, 2007; Elith *et al.*, 2008), the values of learning rate and number of iterations were set as 0.001 and 10000, respectively. Ten-fold cross validation was used to balance model fits and predictive performance.

All the statistical analyses were carried out using R version 3.2.2 (R Core Team, 2015). The lme4 and glmmADMB packages for R were used to perform the LMMs and GLMMs, respectively. The model averaging method and BRTs were achieved using the MuMIn package (Bartoń, 2016) and gbm package (Ridgeway, 2007), respectively.

4.3 Results

4.3.1 Shoot number and shoot length of the lower and upper crown

Primary branches

The difference between the shaded trees and the sunlit trees of the local light intensity of

primary branches was shown in Figure 4.1a. In the upper crown, the local light intensity of branches was significantly higher in the sunlit trees than in the shaded trees. For the lower crown, in contrast, the local light intensity of the branches was stronger in the shaded trees than in the sunlit trees. Similarly, the number of current-year shoots of the lower crown was more in the shaded trees than in the sunlit trees (Figure 4.1b). The median of the number of current-year shoots of the lower crown was 0, indicating that many of primary branches in the sunlit trees did not produce shoots in the lower crown (Figure 4.1b). The difference in the mean lengths of current-year shoots in the lower crown was not significant between the sunlit and the shaded trees (Figure 4.1c).

Secondary branches

Secondary branches indicated almost the same results as in the primary branches (Figure 4.2). In the lower crown, the relative light intensity (Figure 4.2a) and shoot number (Figure 4.2b) were less in the sunlit trees than in the shaded trees, while the shoot lengths were not different between them (Figure 4.2c).

4.3.2 Effects of light intensity, the crown light status and branch position on branch growth and death

Primary branches

To assess the effects of the crown light status and the local light conditions on the growth of primary branches, I investigated the effects of $\ln(rPPFD)$ on shoot number and mean shoot length by considering the difference between the shaded and sunlit trees. This analysis was made for the upper and lower crowns separately, as the relationship between

the crown light status and rPPFD showed different tendency between the upper and lower crowns (Figure 4.1a). In both the upper and lower crowns, the local light intensity $\ln(\text{rPPFD})$ had significant effects on shoot number and shoot length (Table 4.2), but the effects of the crown light status were not significant (Table 4.2). Hence, I pooled all the data of the sunlit and shaded trees, and further investigated effects of the local light conditions $\ln(\text{rPPFD})$ and the primary branch position in a crown (L_{CB}) on the shoot number and mean shoot length (Table 4.3). It indicates that both $\ln(\text{rPPFD})$ and L_{CB} had significant effects on the shoot number and mean shoot length per primary branch (Table 4.3).

As shown in Figure 4.4a, the relationship between the shoot number and the length of a primary branch was not significant. This suggests that the size of a primary branch was not related to its the number of current-year shoots on it. Incidentally, the length of a primary branch increased with decreasing primary branch position (L_{CB}) (Figure 4.4b), indicating a general trend that the length of a primary branch was longer as it is closer to the crown base.

The probability of death of primary branches was significantly affected by the local light conditions (Table 4.4a), but the effect of the crown light status (sunlit or shaded) was not significant (Table 4.4a). In contrast, both $\ln(\text{rPPFD})$ and L_{CB} were significant for the probability of death of a primary branch (Table 4.4b).

Secondary branches

Table 4.5 shows that local light intensity above secondary branches had positive effects on the number and the mean length of current-year shoots per secondary branch in each part on a primary branch. Furthermore, for the shoot number at the distal part (Table 4.5a),

the effect of the crown light status was significant (Table 4.5a). This result is illustrated in Figure 4.5a in the relationship between $\ln(\text{rPPFD})$ and the number of current-year shoots per secondary branch, where the equations for the sunlit and shaded trees were calculated from Table 4.5a, as follows:

$$N_{\text{sunlit}} = \exp(0.27 + 0.99x) \quad (4.4)$$

$$N_{\text{shaded}} = \exp(1.01 + 0.84x) \quad , \quad (4.5)$$

where x is $\ln(\text{rPPFD})$. Because of this significant effect of the crown light status (Table 4.5a), Figure 4.5a illustrates that, at the distal part, the number of shoots produced by sunlit trees was significantly less than that of shaded trees when data of a similar rPPFD levels were compared. However, as the coefficients of x in Eqs 4 and 5 (Table 4.5a) indicate, the rate of increase in shoot number per unit increase of $\ln(\text{rPPFD})$ were greater in sunlit trees than in shaded trees. This indicates that the number of shoots of the former increases more sharply than does shaded trees with increasing rPPFD. In contrast, in the middle and the proximal parts, the effects of the crown light status on the number of shoots were not significant (Tables 4.5c,e and Figures 4.5c, e).

For the effects on the mean shoot length per secondary branch, the crown light status was not significant in the three parts (Tables 4.5b, d; Figures 4.5b,d). For the proximal part, the interaction term was significantly positive (Table 4.5f). According to the estimated parameters in Table 4.5f, the relationship between the local light intensity and shoot length was shown for each of the shaded and sunlit trees in Figure 4.5f. The equations for the shaded and sunlit trees were:

$$L_{\text{shaded}} = \exp(0.27 + 0.52x) \quad (4.6)$$

$$L_{\text{sunlit}} = \exp(0.06 + 1.22x) \quad , \quad (4.7)$$

where x is $\ln(\text{rPPFD})$. The slope of the shaded tree was only 42.6% of sunlit trees. This difference is expressed in Figure 4.5f, in which the mean shoot length per secondary branch was longer in the sunlit trees than in the shaded trees in the range of $\text{rPPFD} > \text{ca. } 5\%$.

As for the probability of the death of secondary branches, the effect of local light condition was significant, whereas the crown light status was not significant, in each of the secondary branch location on a primary branch (Tables 4.6a,b,c).

4.3.3 Relative influences of light intensity, branch position, crown section and crown light status

For the number and the mean length of current-year shoots on primary branches, the relative influence of light intensity was greater than the relative influence of the branch position (Figure 4.6a). For the probability of death of a primary branch, branch position and light intensity indicated almost equal relative influences. As a result, the relative influence of branch position on the probability of primary branch death was greater than those of shoot number and mean shoot length (Figure 4.6a). This result indicates the importance of branch position as a factor affecting branch dynamics. The relative influences of the crown light status and the crown section were all less than 10%. As for secondary branches, the relative influence of light intensity on the shoot number, shoot length and probability of death of secondary branches all exceeded 65% (Figure 4.6b), which was much greater than the contributions of branch position, crown section and

crown light status.

4.4 Discussion

Results showed that local light conditions had significant effects on the shoot number and shoot length of branches (Tables 4.2 and 4.4), which are consistent with previous studies (Stoll & Schmid, 1998; Goulet *et al.*, 2000; Takenaka, 2000; Osada *et al.*, 2014; Larbi *et al.*, 2015). In addition, the effects of crown light status on shoot number and mean shoot length were not significant in the primary branches (Table 4.2 and Figure 4.3). However, as for the secondary branches, the number of current-year shoots at the distal part on sunlit trees was less than on the shaded trees (Figure 4.5a, Table 4.5a), but the rate of the shoot-number increase with increasing rPPFD (the curvature of the curve in Figure 4.5a) was steeper (Table 4.5a) than shaded trees. This suggests that production of current-year shoots of sunlit trees is promoted only under lighter conditions. This result is regarded as a realization of correlative inhibition (Stoll & Schmid, 1998; Sprugel, 2002). Because the phenomenon relating to correlative inhibition was only observed for the level of secondary branches, correlative inhibition may be branching-unit dependent.

While branch position had significant effect on the probability of death of primary branches (Table 4.4b), the relative influence of branch position was stronger on the probability of branch death than on shoot number and shoot length (Figure 4.6a). In contrast, for secondary branches, light intensity was the most influential factor for both the growth and death of secondary branch (Figure 4.6b). It suggests that the growth and death of secondary branches may be mainly determined by its own local light conditions. Figure 4.6 suggests that patterns of growth and death of branches in response to light may

vary by the size of organization levels of branching unit (De Kroon *et al.*, 2005; Kawamura, 2010).

Taken altogether, this study suggests that branch autonomy and correlative inhibition are branching unit dependent; light is important in local scales such as secondary branch levels, while branch position was more influential in a larger scale such as primary branch levels, especially for branch death.

Chapter 5

Growth of Epicormic Shoots

5.1 Introduction

Tree crown is a combination of branches, leaves and flowers directly attached to the main stem (Kozłowski *et al.*, 1997), which enables a tree to display leaves so that leaves can better capture light for photosynthesis. Crown architectural development is intimately linked to the regeneration of branches (Maillette, 1982). Within a tree crown, branches generally originate from sequential growth of apical buds (hereafter “sequential branches”) (Nicolini *et al.*, 2003). However, branches that form from a suppressed or adventitious bud, that is, epicormic branches, have been documented in many species as well (Bégin & Filion, 1999; Ishii & Ford, 2001; Waters *et al.*, 2010). Epicormic branches generally occur as a response to stressful environmental conditions, including wind damage (Cooper-Ellis *et al.*, 1999), fire (Burrows, 2008; Waters *et al.*, 2010), insect outbreaks (Landsber & Ohmart, 1989; Marsh & Adams, 1995), severe drought (Davidson & Reid, 1989; Burrows, 2002), and frost events (Bégin & Filion, 1999). Therefore, the degree of epicormic shoot production has been proposed as an indicator of tree vigor (Nicolini *et al.*, 2003; Colin *et al.*, 2008). However, other studies demonstrated that epicormic sprouting can also occur as a normal and an integral part of crown architectural development and a strategy to prolong tree longevity for some coniferous species in situ (Ishii & Ford, 2001; Ishii & McDowell, 2002; Ishii *et al.*, 2007). Therefore, further research is needed to investigate the role of epicormic branches in crown development and tree growth.

In previous studies, light has been shown to play a fundamental role in the initiation of epicormic sprouting. For example, many studies have demonstrated that epicormic sprouting occurs after pruning, which contributes to a sudden increased light

availability (Kerr & Harmer, 2001; Deal *et al.*, 2003; Gordon *et al.*, 2006; Takiya *et al.*, 2010). Moreover, reducing the light levels in stand through planting shade-tolerant oak species can effectively prevent the production and development of epicormic branches (Fricke *et al.*, 1980; Morisset *et al.*, 2012). In natural stands, local light conditions of branches vary within a tree crown (Niinemets, 2007).

An evergreen conifer, *Picea glehnii* not only survives at extremely low temperatures in winter but also grows in diverse and severe environmental conditions (Sakai & Okada, 1971; Kayama *et al.*, 2007; Bae *et al.*, 2010). During the field work in the studies of Chapters 3 and 4, I observed that *Picea glehnii* species was able to produced epicormic shoots as well. Epicormic shoots were identified by their internodal position on the parent shoot, vertical angle of attachment, or age difference (Ishii & Ford, 2001). It is still uncertain whether the nature of epicormic shoot is related to the ecological characteristics of *P. glehnii*. Previous research has demonstrated that light heterogeneity has significant effect on the growth and death of sequential branches (Chen & Sumida, 2017). The influence of light heterogeneity within a tree crown on epicormic sprouting of Sakhalin spruce also remains unclear.

In this study, I investigated the effects of light intensity and morphological factors on the production of epicormic shoots, compared the production of epicormic branches between sunlit and shaded trees, and attempted to clarify whether the role of epicormic branches in the growth of Sakhalin spruce trees.

5.2 Methods

5.2.1 Field Measurements

Refer to Chapter 4.2.1.

5.2.2 Light Measurements

Refer to Chapter 4.2.2.

5.2.3 Statistical Analysis

The effects of L_{CB} (cm) and natural-log transformed rPPFD (%) (hereafter ‘ln(rPPFD)’) on shoot production were analyzed using generalized linear mixed models (GLMMs). I employed ln(rPPFD) and L_{CB} as the fixed effects, and individual trees as the random effect. The model is expressed as follows:

$$\ln(y_{ij}) = \alpha_0 + \alpha_1 x_{1ij} + I_i, \quad (5.1)$$

where y_{ij} is the number of current-year epicormic shoots produced by primary branch j of tree i ; x_{1ij} represents the ln(rPPFD) or L_{CB} of branch j of tree i , respectively; α_0 and α_1 are the coefficients of fixed effects; I_i is the random intercept within tree i . Because the data of the response variable included many zero data values (i.e., many primary branches with no current-year epicormic shoot production), negative binomial distribution was assumed for the response variable to deal with overdispersion (Zeileis *et al.*, 2008).

The effects of L_{CB} (cm) and ln(rPPFD) on the shoot extension growth of primary branches were analyzed using linear mixed models (LMMs). The response variable was

the mean current-year epicormic shoot length (cm), the fixed and random effects were the same as in Eq. (5.1). The model is expressed as follows:

$$y_{ij} = \beta_0 + \beta_{1ij}x_{1ij} + I_i \quad , \quad (5.2)$$

where y_{ij} is the mean length of current-year epicormic shoots of primary branch j of tree i ; x_{1ij} represents the $\ln(\text{rPPFD})$ and L_{CB} of branch j of tree i , respectively; β_0 and β_1 are the coefficients of fixed effects; I_i is the random intercept within tree i .

In addition, effects of crown light status (i.e., sunlit or shaded) on the number of current-year epicormic shoots and on the length of current-year epicormic shoots (cm) were analyzed using Eq. (5.1) and Eq. (5.2), respectively. The crown light status, a categorical variable with two levels: sunlit and shaded, was the fixed effect, and the number or the length of current-year epicormic shoots was the response variable. All the statistical analyses were carried out using R version 3.2.2 (R Core Team, 2015). The lme4 and glmmADMB packages were used to perform the LMMs and GLMMs, respectively.

5.3 Results

Table 5.1 shows the effect of local light intensity and branch position on the production of current-year epicormic shoots. Results showed that both rPPFD (%) and branch position had no significant effect on the number of current-year epicormic shoots (Table 5.1). In addition, both light intensity and branch position had no significant impact on the length of current-year epicormic shoots (Table 5.2).

On the contrary, crown light status had significant effect on the production of current-year epicormic shoots of primary branches. A primary branch on a shaded tree

produced more current-year epicormic shoots than that on a sunlit tree (Figure 5.1). In contrast, the difference in the mean length of current-year epicormic shoots between shaded trees and sunlit trees was not significant (Figure 5.2).

5.4 Discussion

Results showed that the epicormic sprouting was not related to local light intensity of branches (Table 5.1a). Therefore, the epicormic shoot in the crown of Sakhalin spruce can be considered as a normal function part in the crowns of Sakhalin spruce. As tree grows taller and larger, the hydraulic conductivity decreases due to the increased length of hydraulic path and xylem conductivity (Cruiziat *et al.*, 2002; Koch *et al.*, 2004; Sperry *et al.*, 2008). In contrast to sequential shoots, epicormic sprouting is often observed to occur on trunk or older branch axes (Ishii & Ford, 2001; Otda & Ishii, 2009; Decombeix *et al.*, 2010; Colin *et al.*, 2012). Due to the shortened length of hydraulic path to new foliage, epicormic shoots may significantly increase hydraulic conductance and mitigate the limitation of hydraulic conductivity for tree growth (Ishii *et al.*, 2007). If the main function of epicormic shoots is to reduce the hydraulic limitation, these primary branches that are close to crown base should produce more current-year epicormic shoots. However, results showed that branch position had no significant effect on the number of current-year epicormic shoots (Table 5.1b). Therefore, the release of dormant epicormic buds in the crowns of Sakhalin spruce may not be able to mitigate the hydraulic limitation of the Sakhalin spruce trees.

Furthermore, a primary branch on shaded trees produced more current-year epicormic shoots than sunlit trees, that is, branches on less vigorous trees have a higher tendency to produce epicormic shoots (Figure 5.1). Thus, the number of epicormic shoots may be used as an indicator of tree vigor (Nicolini *et al.*, 2003). Taken altogether, the production of epicormic shoots occurs as a normal and integral part of crown architectural development and a strategy to prolong tree longevity, especially for those less vigorous Sakhalin spruce trees (Ishii & Ford, 2001; Ishii & McDowell, 2002; Ishii *et al.*, 2007).

Chapter 6

General Discussion

6.1 Primary branch

In the entire crown, both light intensity and branch position had significant effect on shoot production, shoot length, and probability of death of primary branches (Tables 3.2, 4.2, and 4.3). Among them, the light intensity had a stronger influence on the shoot production and shoot length of primary branches than branch position (Figure 4.6a). In contrast, the influence of branch position and light intensity on the death of primary branches was approximately equal (Figure 4.6a). Furthermore, in the lower crown, primary branches with stronger light intensity had a tendency to produce more current-year shoots despite the low local light intensity ($rPPFD < ca. 1\%$) (Table 3.2a and Figure 3.1a). In contrast, the probability of death of primary branches in the lower part of crown was affected by branch position, not by light intensity (Table 3.2c and Figure 3.2). These results suggest an importance of the location of branch within a crown on branch dynamics.

As naturally produced chemical compounds within plant tissues, plant hormones such as auxins play a significant role in regulating the growth and development of plants (Powell, 1987; Davies, 2010). In the growing season, auxin concentration is reported to increase with the rise of branch position within tree crown (Uggla *et al.*, 1998). In addition to plant hormones, previous studies suggested that the hydraulic conductivity of branches is also higher in upper crown than that in lower crown (Kupper *et al.*, 2006; Sellin & Kupper, 2007; Yoshimura, 2011). Therefore, the plant hormones and hydraulic conductance associated with branch position within tree crown could explain why the length from the crown base was related to primary branch death.

Another related idea that can explain the importance of branch position in the death of primary branch is the resources allocation (Dewar *et al.*, 2012; Buckley *et al.*,

2013). When branches in the upper part of the crown are growing vigorously under sunlit conditions and resources such as nitrogen are limited, the resources stored in the older part of the crown are translocated to the vigorously growing part so as to repay the invested resources and increase the benefits (Han & Chiba, 2009; Marty *et al.*, 2009; Millard & Grelet, 2010; Dewar *et al.*, 2012; Buckley *et al.*, 2013). Therefore, primary branches with higher branch position may be allotted more resources than those with lower position.

These findings indicate that, due to the critical role of branch position within tree crown, local light intensity alone cannot completely explain the growth and death of primary branches in the crowns of Sakhalin spruce .

6.2 Secondary branch

As with primary branches, light intensity showed significant effects on the growth and death of secondary branches (Table 4.5). In addition, in the lower crown, the secondary branches at the distal part not only produced more current-year shoots (Table 3.4a) but also exhibited a lower probability of death than those at the proximal part (Table 3.4c). In addition, the relative influence of light intensity on shoot production, shoot length and the death of secondary branches all exceeded 65% (Figure 4.6b), which suggests that both the growth and survival of a secondary branch depended mainly on its own local light intensity. Meanwhile, I found that secondary branches at the distal part of primary branches on sunlit trees produced less current-year shoots than those on sunlit trees when branches of a similar light levels were compared (Table 4.5a and Figure 4.5a), whereas

the number of current-year shoots increased sharply on sunlit trees than on shaded trees as light intensity increased (Table 4.5a and Figure 4.5a). This result suggest that shoot production in the sunlit trees were restricted when a branch was under a dark condition and therefore it can be explained by the correlative inhibition among secondary branches (Stoll and Schmid 1998; Sprugel 2002).

When buds or shoots exist at a lighter conditions within a plant, they function strong sink of the nutrients necessary for the growth of the buds or shoots. Then shoots in poor light conditions in the same individual are thought to be actively killed and the resources of the killed shoots are translocated to the sink organs in the same plant and used for their growth (Novoplansky et al. 1989). In other words, correlative inhibition is likely to function as a plant's strategy of efficiently utilizing limited resources.

The correlative inhibition of shoot growth in response to local light conditions is probably mediated by the same hormonal signals in apical dominance (Li & Bangerth, 1999; Kawamura, 2010). Apical dominance is defined as the inhibition of lateral buds activity by the apical bud (Cline, 1994). It has been recognized that basipetally transported auxin from apical buds plays an important role in the inhibition of lateral buds, although the function of auxin in apical dominance is not yet completely understood (Li & Bangerth, 1999; Cline & Sadeski, 2002; Kebrom, 2017). Previous studies using herbaceous plants with two equal shoots: one shoot was under the light (sunlit shoot) and the other in the dark (shaded shoot) demonstrated that the growth of shaded shoot would be inhibited until the sunlit shoot was removed (Snow, 1931; Novoplansky *et al.*, 1989). Li and Bangerth (1999), using two-branched pea plants, found that polarly transported auxin played a primary role in the correlative inhibition between the two branches, and

therefore suggest that the correlative inhibition is similar to the underlying mechanism of apical dominance. In addition to auxin, abscisic acid may act as a correlative inhibitor in shoot growth (White & Mansfield, 1977; Cline & Oh, 2006). Therefore, auxin and some related plant hormones could be involved in the observed correlative inhibition of shoot growth in response to local light conditions in Sakhalin spruce (Novoplansky *et al.*, 1989; Li & Bangerth, 1999; Kawamura, 2010).

6.3 Comparison of primary and secondary branch

Results showed that local light intensity had a significant effect on the shoot number and mean shoot length of primary and secondary branches (Tables 4.2 and 4.5). For primary branches, the differences between shaded and sunlit trees in shoot number and mean shoot length were not significant (Table 4.2). However, for secondary branches, the difference between the sunlit and shaded trees in shoot number was significant at the distal part (Figure 4.5a, Table 4.5a). This result is regarded as a realization of correlative inhibition (Stoll & Schmid, 1998; Sprugel, 2002). Because the phenomenon relating to correlative inhibition was only observed in a relatively small unit of branching, correlative inhibition may be branching-unit dependent.

Moreover, the relative influence of light on the growth and death of branches were different between these two branching units (Figure 4.6). In primary branches, shoot number and shoot length were mainly affected by local light intensity, whereas the probability of death of a primary branch was equally affected by both local light condition and the primary branch position within a crown (Figure 4.6a). Similarly, death of primary

branches in the lower part of crown under a low range of rPPFD (< 3%) was significantly affected by branch position, but the effect of local light intensity on branch death was not significant (Figure 3.1). In contrast to primary branches, light intensity was the most influential factors for both the growth and death in secondary branch (Figure 4.6b). Therefore, effects of light on the growth and survival of branches may depend on the size of organization levels of branching unit as well (De Kroon *et al.*, 2005; Kawamura, 2010).

6.4 Growth of epicormic shoots

Results showed that light had no significant effect on the number of current-year epicormic shoots on primary branches (Table 5.1). However, primary branches on shaded trees produced more current-year epicormic shoots than those on sunlit trees, that is, branches on less vigorous trees have a higher tendency to produce epicormic shoots (Figure 5.1). This findings suggest that epicormic shoots may be a normal function part in the crowns of Sakhalin spruce, and the number of epicormic shoots may be used as an indicator of tree vigor (Nicolini *et al.*, 2003). Therefore, the production of epicormic shoots occurs as a normal and an integral part of crown architectural development and may be a complementary strategy to prolong tree longevity, especially for those less vigorous Sakhalin spruce trees (Ishii & Ford, 2001; Ishii & McDowell, 2002; Ishii *et al.*, 2007).

6.5 Conclusions

In summary, this study suggests that (i) light intensity cannot completely explain the growth and survival of branches, (ii) growth of secondary branches may be inhibited when others are under a stronger light intensity within the same crown, (iii) branch autonomy and correlative inhibition are branching unit dependent, that is, light is important in local scales such as secondary branch levels, while branch position was more influential in a larger scale such as primary branch levels, especially for branch death, and (iv) growth of epicormic shoots is an adaptive growth strategy in the development of crown architecture to maintain the crown of Sakhalin spruce. Trees with this branching unit dependent plasticity as well as epicormic shoots in response to various abiotic and biotic conditions, such as shade, inter- or intra-competition, and herbivore attack, would be more flexible to exploit resources and survive in severe natural environment conditions (Kawamura, 2010).

Because this study only considered morphological process, further research considering underlying physiological mechanisms (e.g., resources allocation, plant hormones) for this observed branching unit dependent plasticity and initiation of epicormic shoots is needed to better understand the dynamics of the formation and maintenance of crown architecture. Furthermore, comparative studies in the response of architectural units to environment conditions among species is critical to clarify the mechanisms behind species coexistence and the functions of mixed forests (Kohyama *et al.*, 2003; Ishii & Asano, 2010). Therefore, it is also necessary to identify and understand whether the observed branching-unit dependent plasticity exist in other coniferous or broadleaved species in mixed forests.

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Table 3.1. Individual sizes of 16 sample trees. Status = 1 represents trees that died between July 2013 and July 2014; otherwise status = 0. DBH, diameter at breast height; H_{CB} , height of the crown base.

Tree ID	Status	DBH (cm)	H_{CB} (m)	Height (m)
1	1	7.0	4.37	7.02
2	1	7.1	3.42	5.88
3	1	7.6	2.68	6.00
4	0	8.3	2.97	6.74
5	0	8.6	3.44	8.00
6	1	8.9	4.45	7.54
7	0	9.6	3.54	9.00
8	1	9.6	3.29	6.93
9	0	10.5	3.43	8.81
10	0	10.5	3.12	8.19
11	0	10.8	4.24	9.26
12	0	12.1	4.11	9.63
13	0	13.3	4.01	9.85
14	0	13.4	3.85	10.04
15	0	13.4	3.45	12.63
16	0	15.9	3.76	12.05

Table 3.2. Coefficients of the effects of relative photosynthetic photon flux density (rPPFD) (%) and the length between the basal location of a primary branch and the crown base (L_{CB} , cm) on (a) the probability (P) of current-year shoot production on a primary branch (see Figure 1); (b) the length of current-year shoots of primary branches; and (c) the probability (P) of death of primary branches (see Figure 3.2).

(a) Shoot production of primary branches ($n = 64$)

	Estimate	Standard error	z value	p value
Intercept	0.01	0.29	0.03	0.97
$\ln(\text{rPPFD})$	0.62	0.24	2.57	0.01
	Estimate	Standard error	z value	p value
Intercept	-0.90	0.59	-1.52	0.13
L_{CB}	0.01	0.01	1.06	0.29

(b) Length of current-year shoot of primary Branches ($n = 26$)

	Estimate	Standard error	t value	p value
Intercept	2.08	0.3	7.05	0.00
$\ln(\text{rPPFD})$	-0.05	0.12	-0.44	0.66
	Estimate	Standard error	t value	p value
Intercept	2.23	0.21	10.56	0.00
L_{CB}	0.00	0.00	-0.21	0.83

(c) Probability of death of primary branches ($n = 44$)

	Estimate	Standard error	z value	p value
Intercept	0.35	0.43	0.81	0.42
$\ln(\text{rPPFD})$	-0.35	0.26	-1.33	0.18
	Estimate	Standard error	z value	p value
Intercept	2.81	1.15	2.44	0.02
L_{CB}	-0.04	0.02	-2.10	0.04

Table 3.3. The regression between relative photosynthetic photon flux density ($\ln(\text{rPPFD})$) and the length between the crown base and the base of primary branch (L_{CB}) in (a) 2013 and (b) 2015. The data of rPPFD (%; the response variable) were log-transformed to meet the assumption of normal residuals.

(a) 2013 ($n = 24$)

	Estimate	Standard error	t value	p value
Intercept	-1.27	0.48	-2.61	0.03
L_{CB}	0.01	0.00	1.24	0.23

(b) 2015 ($n = 24$)

	Estimate	Standard error	t value	p value
Intercept	0.07	0.38	0.18	0.86
L_{CB}	0.00	0.00	0.90	0.38

Table 3.4. Results of generalized linear mixed models concerning the effects of secondary branch position on (a) the number of current-year shoots on secondary branches (see Figure 3.3), (b) the mean length of current-year shoots on secondary branches (see Figure 3.4), and (c) the probability of death of a secondary branch. The predictor (position) was a categorical variable having three parts (Distal, Middle, and Proximal), where α corresponds to the estimates of the Distal, $\alpha + \beta_1$ to the Middle, and $\alpha + \beta_2$ to the Proximal parts.

(a) Number of current-year shoots on a secondary branch ($n = 121$)

	Estimate	Standard error	z value	p value
α	2.05	0.31	6.53	0.00
β_1	-0.80	0.40	-2.03	0.04
β_2	-1.98	0.47	-3.64	0.00

(b) Mean length (cm) of current-year shoots of secondary branches ($n = 64$)

	Estimate	Standard error	t value	p value
α	2.22	0.16	13.76	0.00
β_1	-0.20	0.12	-1.69	0.10
β_2	0.07	0.17	0.45	0.66

(c) Probability of death of a secondary branch ($n = 60$)

	Estimate	Standard error	z value	p value
α	-2.06	1.60	-1.29	0.20
β_1	0.38	1.21	-0.31	0.76
β_2	3.54	1.58	2.25	0.02

Table 3.5. The effect of secondary branch positions on the relative photosynthetic photon flux density $\ln(\text{rPPFD})$ for secondary branches selected in 2015. The estimates correspond with the mean $\ln(\text{rPPFD})$ s at the Distal, Middle, and Proximal parts, where α corresponds to the estimates of the Distal, $\alpha + \beta_1$ to the Middle, and $\alpha + \beta_2$ to the Proximal parts. The data of rPPFD (%) (the response variable) were transformed into natural logarithm to meet the assumption of normal residuals ($n = 126$).

	Estimate	Standard error	<i>t</i> value	<i>p</i> value
α	0.08	0.33	0.24	0.82
β_1	-0.09	0.06	-1.42	0.16
β_2	-0.57	0.07	-8.45	0.00

Table 4.1 Individual size of the sample trees selected. DBH, diameter at breast height; H_{CB} , height of the crown base; CL, crown length; rPPFD, the relative photosynthetic photon flux density above the top of tree.

Tree ID	DBH (cm)	Height (m)	H_{CB} (m)	CL (m)	rPPFD (%)	Crown status
1	6.83	5.59	380	179	10	shaded
2	8.68	8.55	431	424	34	shaded
3	9.71	10.02	533	469	88	sunlit
4	9.81	8.09	502	307	98	sunlit
5	9.95	7.23	369	354	12	shaded
6	10.57	7.93	397	396	5	shaded
7	10.92	10.3	449	581	93	sunlit
8	12.45	10.12	502	510	12	shaded

Table 4.2 Effects of local light condition of primary branches $\ln(rPPFD)$ and the crown light status (shaded or sunlit) on shoot number and the natural-log transformed mean shoot length of primary branches in the upper and lower crown analyzed by GLMM. “Light” indicates $\ln(rPPFD)$, “Sunlit” indicates the sunlit trees. The “Shaded” level was set as the reference group in the Table. “Sunlit×Light” represents the interaction term. Individual trees were set as the random effects in the model. These results are illustrated in Figure 4.3.

(a) Shoot number in the upper crown (n=61)

	Estimate	SE	z value	p value
Intercept	3.47	0.20	17.22	0.00
Light	0.54	0.09	5.93	0.00
Sunlit	0.14	0.31	0.45	0.65
Sunlit×Light	-0.01	0.21	0.03	0.97

(b) Shoot length in the upper crown (n=58)

	Estimate	SE	z value	p value
Intercept	0.73	0.10	7.19	0.00
Light	0.37	0.04	8.18	0.00
Sunlit	-0.22	0.27	0.81	0.42
Sunlit×Light	0.13	0.11	1.21	0.23

(c) Shoot number in the lower crown (n=65)

	Estimate	SE	z value	p value
Intercept	1.89	0.51	3.63	0.00
Light	1.48	0.26	5.57	0.00
Sunlit	-0.05	0.93	0.06	0.96
Sunlit×Light	0.17	0.56	0.30	0.76

(d) Shoot length in the lower crown (n=39)

	Estimate	SE	z value	p value
Intercept	0.22	0.14	1.48	0.14
Light	0.40	0.10	3.98	0.00
Sunlit	0.05	0.26	0.18	0.86
Sunlit×Light	0.24	0.28	0.83	0.41

Table 4.3 Effects of local light condition of primary branches $\ln(\text{rPPFD})$ and primary branch location (the length between the basal location of a primary branch and the crown base L_{CB} , m) on shoot number and the natural-log transformed mean shoot length of primary branches analyzed by GLMM. “Light” indicates $\ln(\text{rPPFD})$, “Light \times L_{CB} ” represents the interaction term. Individual trees were set as the random effects in the model.

(a) shoot number ($n=126$)				
	Estimate	SE	z value	p value
Intercept	1.78	0.37	4.82	0.00
Light	1.31	0.22	5.82	0.00
L_{CB}	0.58	0.20	2.81	0.00
Light \times L_{CB}	-0.24	0.08	2.86	0.00

(b) shoot length ($n=97$)				
	Estimate	SE	z value	p value
Intercept	0.12	0.11	1.05	0.29
Light	0.31	0.06	5.39	0.00
L_{CB}	0.25	0.05	4.86	0.00
Light \times L_{CB}	0.04	0.04	1.06	0.29

Table 4.4 Effects of the local light conditions $\ln(rPPFD)$ of primary branches and (a) crown light status, and (b) primary branch location (the length between the basal location of a primary branch and the crown base L_{CB} , cm) on probability of death for primary branches analyzed by GLMM. “Light” indicates $\ln(rPPFD)$, “Sunlit×Light” and “Light× L_{CB} ” represent the interaction term. Individual trees were set as the random effects in the model.

(a) Effects of light and crown light status ($n=126$)

	Estimate	SE	z value	p value
Intercept	-2.26	1.15	1.95	0.05
Light	-2.40	0.82	2.90	0.00
Sunlit	-0.07	1.93	0.03	0.97
Sunlit×Light	-1.39	1.59	0.87	0.39

(b) Effects of light and branch position ($n=126$)

	Estimate	SE	z value	p value
Intercept	-0.68	1.17	0.58	0.56
Light	-1.99	0.97	2.04	0.04
L_{CB}	-0.02	0.01	2.16	0.03
Light× L_{CB}	-0.01	0.01	1.09	0.28

Table 4.5 Effects of the local light conditions $\ln(rPPFD)$ and the crown light status (shaded or sunlit) on the number and the natural-log transformed mean length of current-year shoots on secondary branches at the distal, middle and proximal parts of primary branches analyzed by GLMM results. “Light” indicates $\ln(rPPFD)$, “Sunlit” indicates the sunlit trees. The “Shaded” level was set as the reference group in the Table. “Sunlit×Light” represents the interaction term. Individual trees were set as the random effects in the model. These results are illustrated in Figure 4.5.

(a) Shoot number at the distal ($n=250$)					(b) Shoot length at the distal ($n=166$)			
	Estimate	SE	z value	p value	Estimate	SE	z value	p value
Intercept	1.01	0.27	3.74	0.00	0.34	0.09	3.69	0.00
Light	0.84	0.11	7.65	0.00	0.80	0.09	9.13	0.00
Sunlit	-0.74	0.37	2.01	0.04	0.11	0.19	0.61	0.54
Sunlit×Light	0.15	0.17	0.88	0.38	-0.25	0.17	1.46	0.14

(c) Shoot number at the middle ($n=247$)					(d) Shoot length at the middle ($n=132$)			
	Estimate	SE	z value	p value	Estimate	SE	z value	p value
Intercept	0.44	0.29	1.55	0.12	0.31	0.10	3.11	0.00
Light	0.98	0.12	8.17	0.00	0.70	0.08	8.89	0.00
Sunlit	-0.24	0.50	0.48	0.63	0.19	0.15	1.28	0.20
Sunlit×Light	0.19	0.21	0.87	0.38	0.09	0.15	0.55	0.58

(e) Shoot number at the proximal ($n=242$)					(f) Shoot length at the proximal ($n=83$)			
	Estimate	SE	z value	p value	Estimate	SE	z value	p value
Intercept	-0.12	0.45	0.26	0.80	0.27	0.17	1.56	0.12
Light	1.22	0.27	4.44	0.00	0.52	0.18	2.84	0.00
Sunlit	-0.95	0.79	1.19	0.23	-0.21	0.34	0.61	0.54
Sunlit×Light	0.72	0.38	1.88	0.06	0.70	0.24	2.93	0.00

Table 4.6 Effects of the local light conditions $\ln(rPPFD)$ and the crown light status (shaded or sunlit) on the probability of death for secondary branches (a) at the distal parts, (b) at the middle parts, (c) at the proximal parts of primary branches analyzed by GLMM. “Light” indicates $\ln(rPPFD)$, “Sunlit” indicates the sunlit trees. The “Shaded” level was set as the reference group in the Table. “Sunlit×Light” represents the interaction term. Individual trees were set as the random effects in the model.

(a) The distal parts ($n=250$)				
	Estimate	SE	<i>z</i> value	<i>p</i> value
Intercept	-1.32	0.65	2.01	0.05
Light	-1.68	0.33	5.12	0.00
Sunlit	-0.12	1.20	0.10	0.92
Sunlit×Light	-0.51	0.62	0.82	0.41
(b) The middle parts ($n=247$)				
	Estimate	SE	<i>z</i> value	<i>p</i> value
Intercept	-1.34	0.68	1.96	0.05
Light	-1.52	0.30	4.98	0.00
Sunlit	-0.37	1.24	0.29	0.77
Sunlit×Light	-0.68	0.60	1.12	0.26
(c) The proximal parts ($n=242$)				
	Estimate	SE	<i>z</i> value	<i>p</i> value
Intercept	-0.56	0.40	1.38	0.17
Light	-1.43	0.27	5.17	0.00
Sunlit	-1.10	0.72	1.53	0.13
Sunlit×Light	-0.64	0.50	1.27	0.21

Table 5.1 Effects of (a) local light intensity and (b) branch position on the number of current-year epicormic shoots of primary branches. “ln(rPPFD)”, the natural log-transformed relative photosynthetic photon flux density rPPFD (%); “ L_{CB} (m)”, the length between the base of a primary branch and crown base.

(a) Local light intensity ($n = 97$)

	Estimate	Standard error	z value	p value
Intercept	1.53	0.46	3.36	0.00
ln(rPPFD)	0.24	0.39	0.61	0.54

(b) Branch position ($n = 97$)

	Estimate	Standard error	z value	p value
Intercept	2.05	0.43	4.83	0.00
L_{CB} (m)	-0.17	0.13	-1.34	0.18

Table 5.2 Effects of (a) local light intensity and (b) branch position on the length of current-year epicormic shoots of primary branches. “ln(rPPFD)”, the natural log-transformed relative photosynthetic photon flux density rPPFD (%); “ L_{CB} (m)”, the length between the base of a primary branch and the crown base.

(a) Light intensity ($n = 68$)

	Estimate	Standard error	t value	p value
Intercept	1.50	0.11	13.78	0.00
ln(rPPFD)	0.07	0.12	0.59	0.56

(b) Branch position ($n = 68$)

	Estimate	Standard error	t value	p value
Intercept	1.49	0.11	13.06	0.00
L_{CB} (m)	0.03	0.05	0.66	0.51

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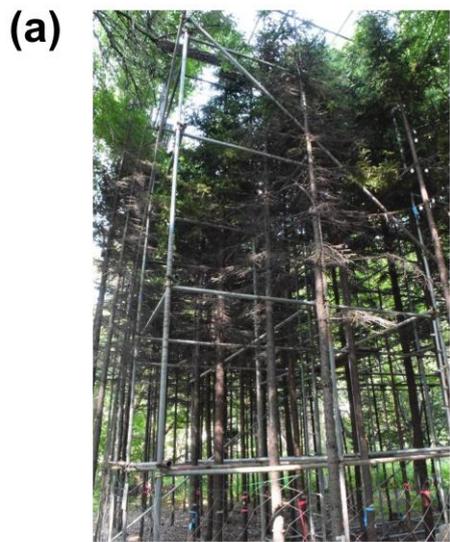


Figure 2.1. The scaffolding constructed in the study site.

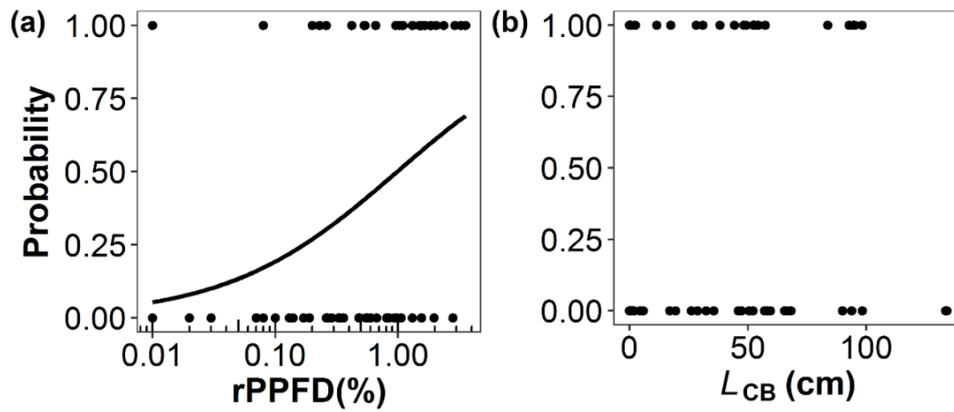


Figure 3.1. Effects of (a) relative photosynthetic photon flux density (rPPFD); and (b) the length between its basal location and the crown base (L_{CB}) on the probability (P) that one or more current-year shoots are produced on a primary branch. The curved line in (a) is represented by Equation (1), and its coefficients are provided in Table 1. In (b), the effects of L_{CB} were not significant ($p = 0.29$; see Table 3.2).

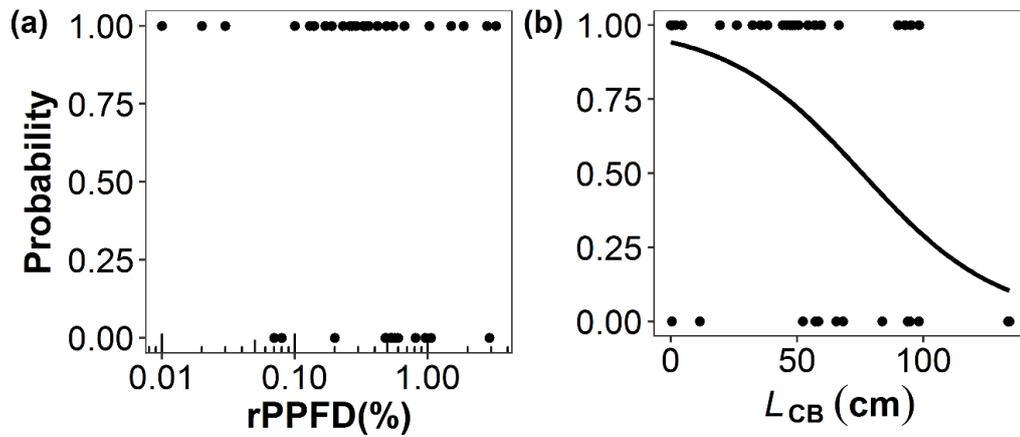


Figure 3.2. Effects of (a) natural-log transformed relative photosynthetic photon flux density ($\ln(\text{rPPFD})$); and (b) the length between the basal location of the primary branch and the crown base (L_{CB} , cm) on the probability of death (July 2013–July 2014) of a primary branch. In (a), the effects of $\ln(\text{rPPFD})$ were not significant ($p = 0.18$; see Table 1). The coefficients of the curved line in (b) showing Equation (1) are given in Table 3.2.

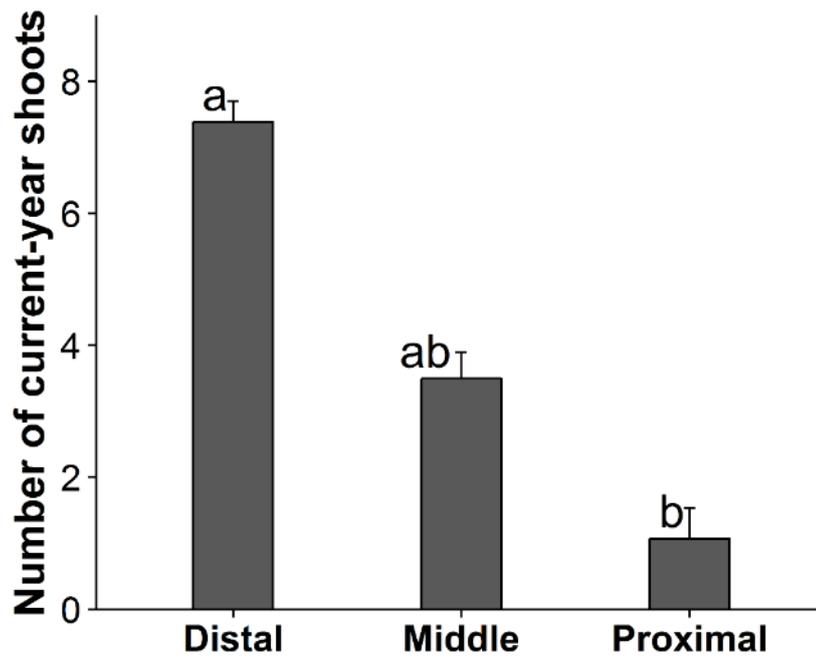


Figure 3.3. Differences in the mean number of current-year shoots per secondary branch among the secondary branch positions. Different letters indicate significant differences between groups ($p < 0.05$; Tukey honest significant difference test). The generalized linear mixed models coefficients are given in Table 3.4. Error bars indicate standard error.

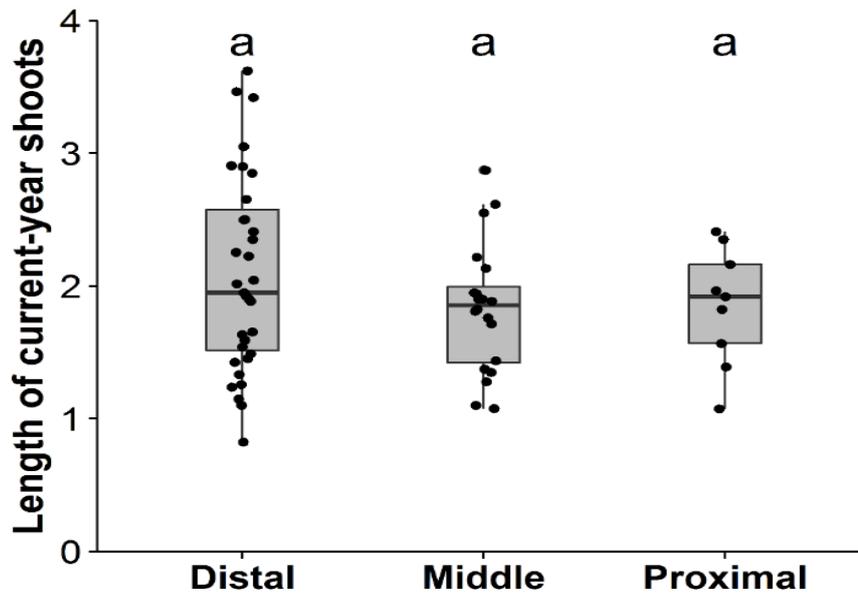


Figure 3.4. Comparison between the secondary branch positions of the mean length of current-year shoots (cm). Closed circles show the data, but the data fluctuated randomly in horizontal directions. The same letter “a” indicate that the differences between groups were not significant ($p < 0.05$, Tukey honest significant difference test). Length of a box indicates the interquartile range, where the horizontal lines inside each box represent the median, and the bottom and top of the box represent the first and third quartiles, respectively. The lower and upper whiskers show 95% confidence intervals. The closed circles outside the boxes represent outliers. The generalized linear mixed models coefficients are given in Table 3.4.

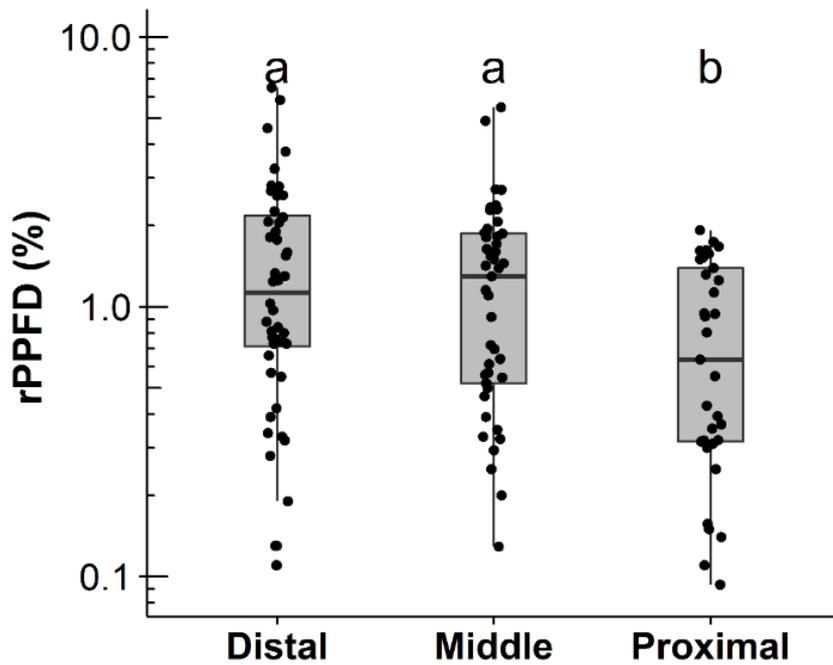


Figure 3.5. Comparisons between the secondary branch positions (distal, middle, and proximal parts of primary branches) of their relative photosynthetic photon flux density $\ln(rPPFD)$. Different letters indicate significant differences between groups ($p < 0.05$, Tukey's honest significant difference test). Length of a box indicates the interquartile range, where the horizontal lines inside each box represent the median, and the bottom and top of the box represent the first and third quartiles, respectively. The lower and upper whiskers show 95% confidence intervals. The closed circles outside the boxes represent outliers. The generalized linear mixed models coefficients are given in Table 3.5.

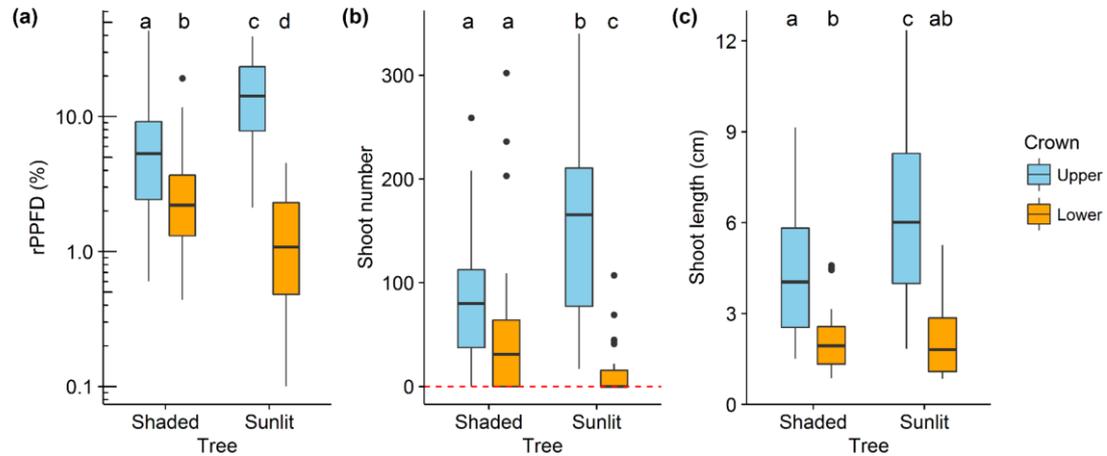


Figure 4.1. Differences between the lower crown of shaded trees, the upper crown of shaded trees, the lower crown of sunlit trees, and the upper crown of sunlit trees in (a) the relative photosynthetic photon flux density (rPPFD), (b) the number of current-year shoots (shoot number), and (c) mean length of current-year shoots (shoot length) of primary branches. The bottom and top of the box represent the first and third quartiles, respectively, and the horizontal lines inside each box represent the median. The lower and upper whiskers show 95% confidence intervals. The closed circles outside the boxes represent outliers. Different letters indicate significant differences between groups ($p < 0.05$, Tukey's honest significant difference test).

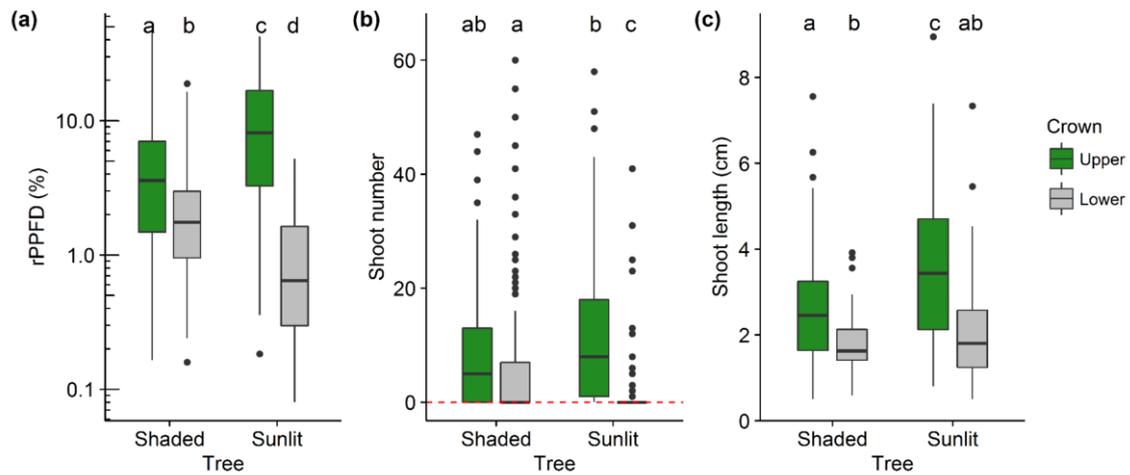


Figure 4. 2. Differences between the lower crown of shaded trees, the upper crown of shaded trees, the lower crown of sunlit trees, and the upper crown of sunlit trees in (a) the relative photosynthetic photon flux density (rPPFD), (b) number of current-year shoots (shoot number), and (c) mean length of current-year shoots (shoot length) of secondary branches. The bottom and top of the box represent the first and third quartiles, respectively, and the horizontal lines inside each box represent the median. The lower and upper whiskers show 95% confidence intervals. The closed circles outside the boxes represent outliers. Different letters indicate significant differences between groups ($p < 0.05$, Tukey's honest significant difference test).

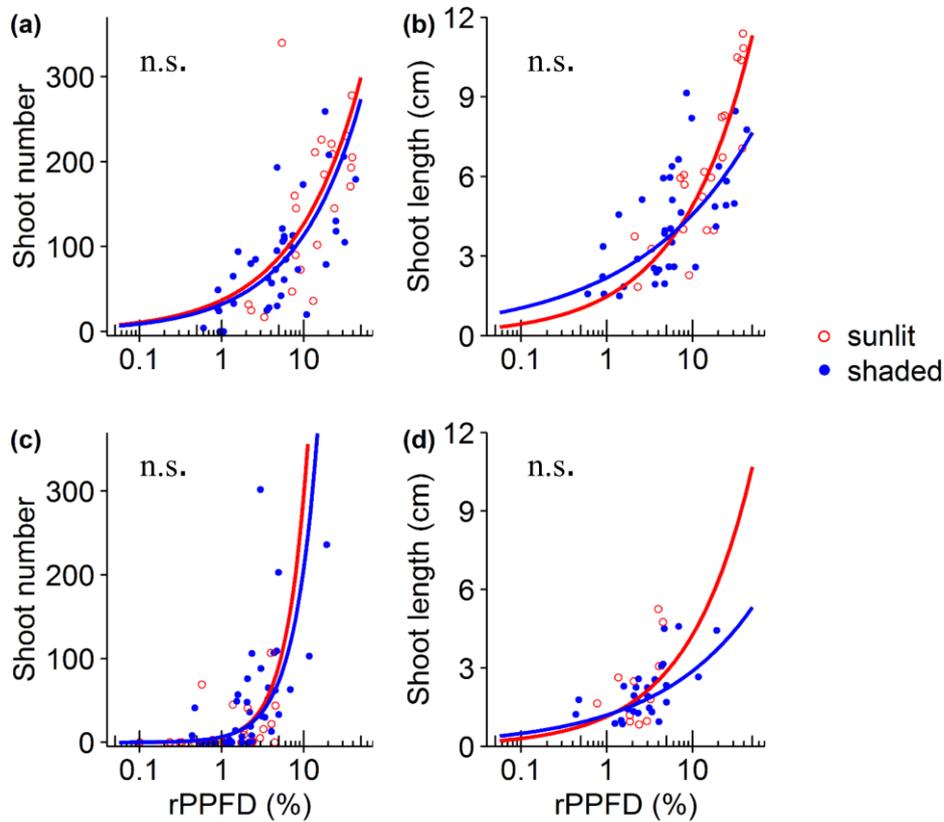


Figure 4.3. Effects of the relative photosynthetic photon flux density $\ln(\text{rPPFD})$ on the shoot number and mean shoot length (cm) per primary branch on shaded and sunlit trees. The closed blue and open red circles represent shaded and sunlit trees, respectively. (a) shoot number in the upper crown, (b) shoot length in the upper crown, (c) shoot number in the lower crown, (d) shoot length in the lower crown. “n.s.” indicates the difference between shaded and sunlit trees was not significant. Shoot length was natural-log transformed in the model and fitted curves were drawn based on the results in Table 4.2.

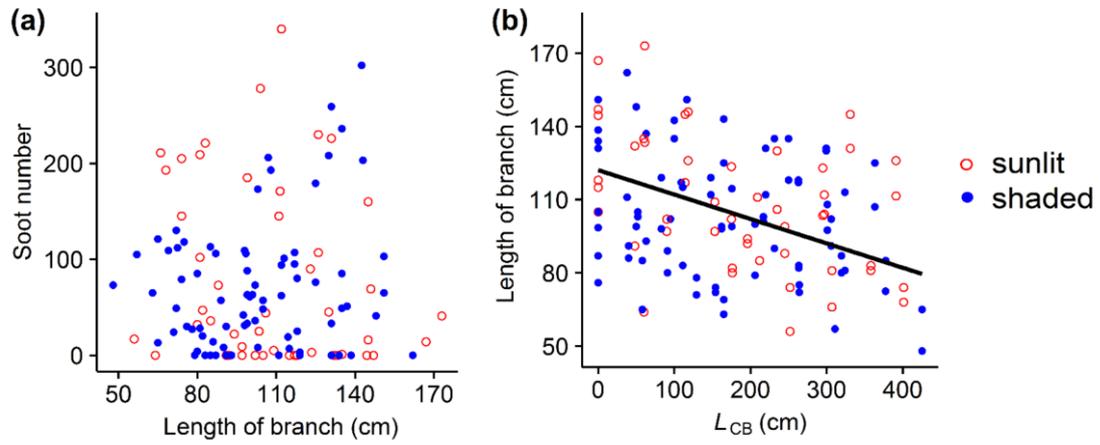


Figure 4.4. Relationship of the length of a primary branch (L , cm), with (a) shoot number, and with (b) the primary branch position (L_{CB} , cm). The closed blue and open red circles represent shaded and sunlit trees, respectively. The equation for the relationship between branch length and branch position is: $L = 122.1 - 0.1 L_{CB}$ ($n=126$, $SE=0.01$, $p < 0.01$).

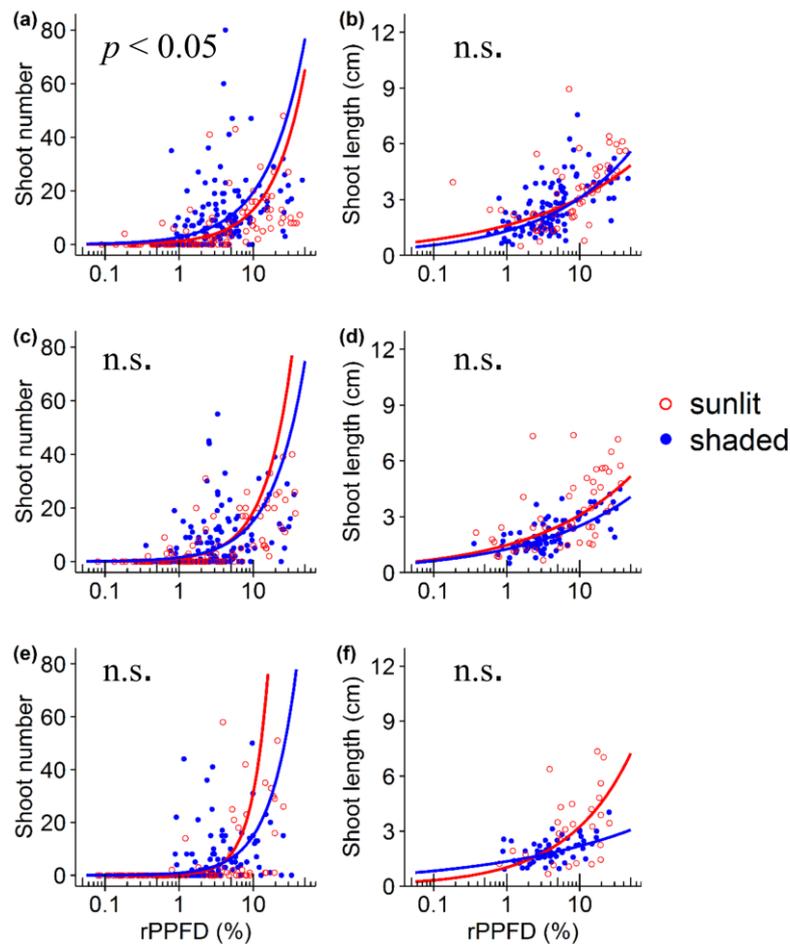


Figure 4.5. Effects of the relative photosynthetic photon flux density $\ln(rPPFD)$ on the shoot number and mean shoot length (cm) of secondary branches at the distal, middle and proximal parts of secondary branches on shaded and sunlit trees. The closed blue and open red circles represent shaded and sunlit trees, respectively. (a) shoot number at the distal, (b) shoot length at the distal, (c) shoot number at the middle, (d) shoot length at the middle, (e) shoot number at the proximal, (f) shoot length at the proximal. “ $p < 0.05$ ” and “n.s.” indicate the difference between shaded and sunlit trees was significant and not significant, respectively. Shoot length was natural-log transformed in the model and fitted curves were drawn on based on the results in Table 4.5.

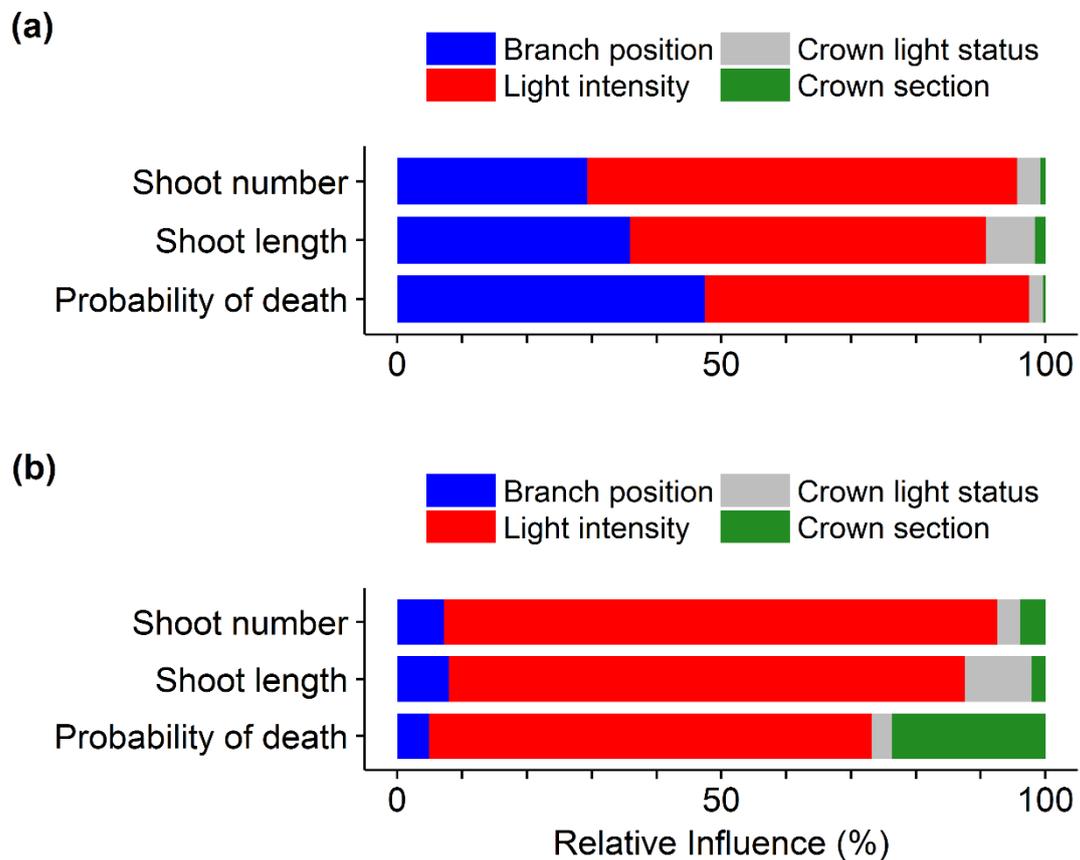


Figure 4.6. Relative influence of the relative photosynthetic photon flux density $\ln(rPPFD)$, branch position, crown section and crown light status (shaded or sunlit) on the shoot number, mean shoot length, and probability of death for (a) primary and (b) secondary branches. The branch position of primary branches was the length between the basal location of a primary branch and the crown base (L_{CB} , cm), and the position of secondary branches was a categorical variable with three levels (the distal, the middle and the proximal).

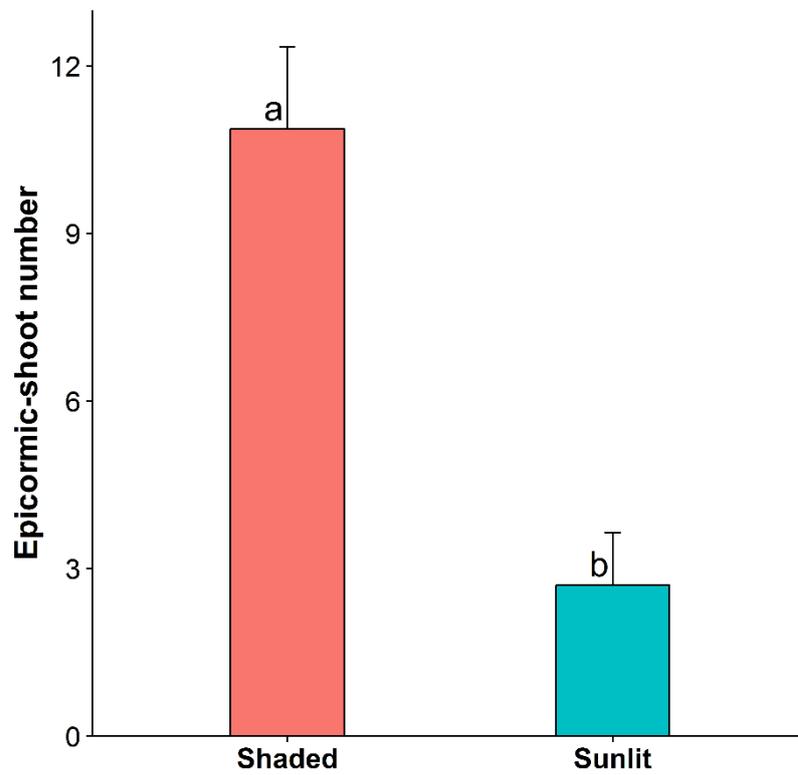


Figure 5.1 Difference in the mean number of current-year epicormic shoots of primary branches on shaded trees and sunlit trees. Different letters indicate significant differences ($p < 0.05$). Error bars indicate standard error.

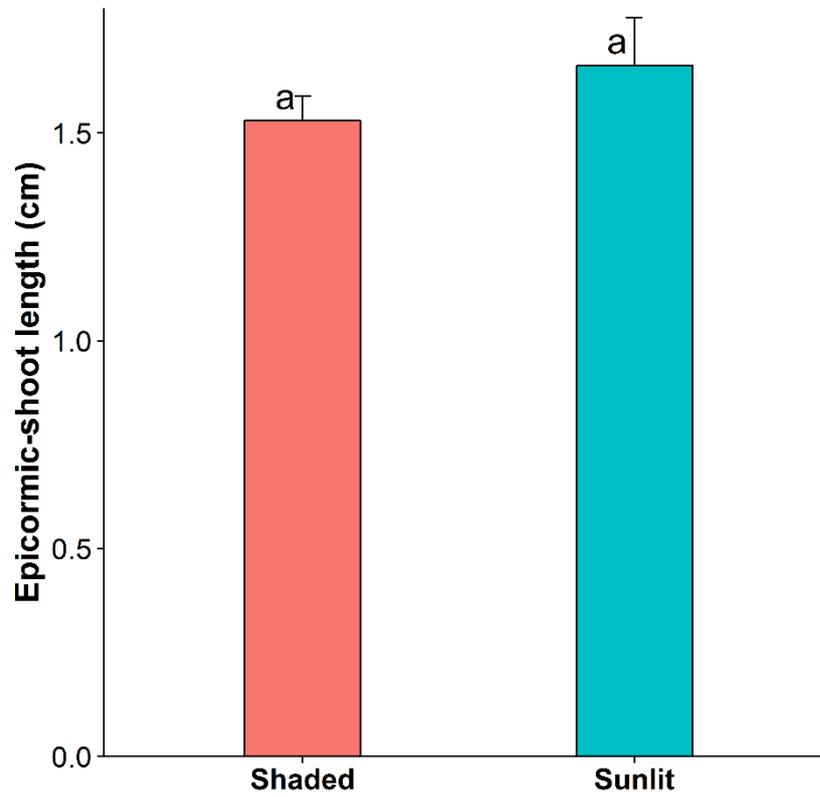


Figure 5.2 Difference in the mean length of current-year epicormic shoots of primary branches on shaded trees and sunlit trees. Different letters indicate significant differences ($p < 0.05$). Error bars indicate standard error.