Long-term crown expansion of *Quercus crispula* in Hokkaido, northern Japan: observation and modeling

Kiyoshi Umeki, Kentaro Tada, En-Mi Lin, and Tsuyoshi Honjo

Graduate School of Horticulture, Chiba University
Matsudo, Chiba 271-8510, Japan
umeki@faculty.chiba-u.jp

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Introduction

Canopy structure is one of the most important factors influencing ecological processes in forest ecosystems. For example, it determines light interception and photosynthesis, transpiration, rain interception, litter production, the modification of environmental conditions under the canopy, and the creation of habitats for various organisms (e.g., Montgomery and Chazdon, 2001; Mariscal et al., 2004). Therefore, a better knowledge of canopy structure and its dynamics is indispensable for clarifying the functions of forest ecosystems and managing forests appropriately.

To understand the structure and dynamics of a forest canopy, elucidating the developmental processes of individual crowns is important because a canopy consists of crowns. We analyzed the crown expansion in an oak forest in Hokkaido, northern Japan, and modeled the crown expansion rate in relation to light availability at the crown surface and individual size based on long-term *in situ* observation of crown dimensions. We used the ray-tracing method to estimate light availability at the crown surface and a linear mixed-effects model to relate crown expansion rate with factors influencing it.

Methods

We placed two plots (25 × 50 m) in a secondary hardwood forest stand in Nishiokoppe, Hokkaido, northern Japan, in 1992. The forest stand was dominated by *Quercus crispula.* One of the plots was heavily thinned in 1994, whereas the other remained intact.

For all trees >5 cm in diameter at breast height (D), we measured tree height (H), height of the live crown base (Hb), and the horizontal distance from trunk base to crown edge (W) in four directions (north, east, south, and west) in 1995, 1999, and 2003 (Fig. 1a). We recorded the coordinates of the trunk base of trees using a two-dimensional coordinate system on slopes where the plots were located and converted them to three-dimensional coordinates using topological data for the slopes.

To express trees in a modeled stand, an individual tree was divided into a crown and a trunk. A crown was modeled by an ellipsoid and a trunk was modeled by a cone whose tip was at the center of the crown ellipsoid (Fig. 1b). Although this representation of trees is rather simple, we used this because it is directly related to the tree measurement. Using this tree model, we visualized the thinned plot as in Fig. 2.

To evaluate horizontal crown expansion, we calculated the change in the horizontal distance from trunk base to crown edge (W) in four directions (changes in the north, east, south, and west directions are denoted as ΔW_N, ΔW_E, ΔW_S, and ΔW_W, respectively) for the intervals 1995–1999 and 1999–2003. In the analysis, ΔW_N, ΔW_E, ΔW_S, and ΔW_W were pooled and denoted as ΔW. To evaluate vertical crown growth, we calculated the change in crown length (ΔL) whereby crown length (L) is tree height (H) minus the height of the live crown base (Hb).

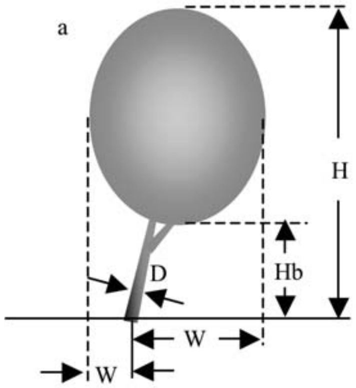

Fig. 1. Schematic diagram of a tree. (a) Measured dimensions of a tree; (b) modeled tree.

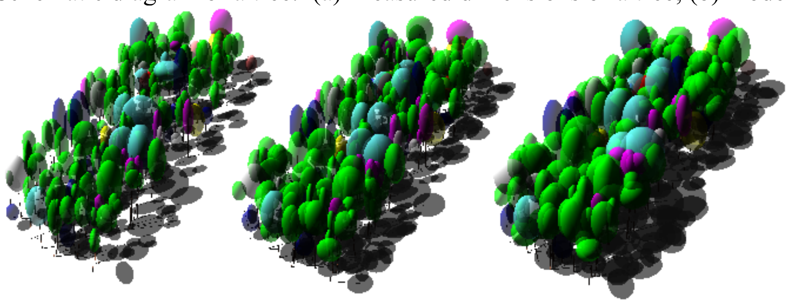

Fig. 2. Three-dimensional visualization of a modeled forest stand for the thinned plot in Nishiokoppe, Hokkaido, northern Japan, in 1995 (left), 1999 (center), and 2003 (right).

Using a ray-tracing method (Sievänen et al., 2000), we calculated canopy openness at 13 points (light sensors) on the surface of the modeled crown as a surrogate of light availability at the points. One light sensor was located at the top of crown. The other light sensors were located on the side surfaces of the crown. Their vertical heights were located at the heights where the distance from the crown base was 1/2, 2/3, and 5/6 of the crown length. At each height, four light sensors were located corresponding to four directions (north, east, south, and west; Fig. 3a). At each light sensor, canopy openness was calculated using 32,768 light beams (128 zenith and azimuth 256 angles); we judged whether each light beam hit crowns or trunks, and evaluated canopy openness as the ratio of the number of light beams that did not hit any objects to the total number of light beams (Fig. 3b).

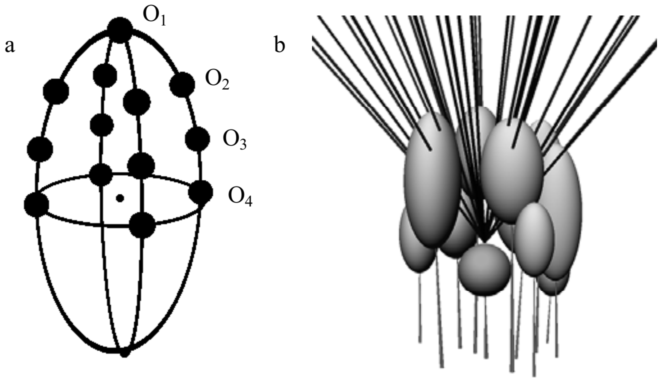

Fig. 3. Method for calculating canopy openness of modeled trees. (a) Positions of light censors on the crown surface of a tree; (b) light beams from a light sensor.

We used a linear mixed-effects model (Pinheiro and Bates, 2000) to construct the relationship between horizontal crown expansion (ΔW) and the explanatory variables of canopy openness at the crown surface for four height levels (O_1–O_4; Fig. 3a), tree height (H), diameter at breast height (D), horizontal distance from the trunk base to the crown edge (W), a qualitative variable representing the effect of different aspects (A; north, east, south, or west), and a binary variable representing the effect of different measurement intervals (I; 1995–1999 or 1999–2003). We considered random variation associated with individual trees and incorporated a random effect (t) into the model. Therefore, the full model was

$$\Delta W = a_0 + a_1O_1 + a_2O_2 + a_3O_3 + a_4O_4 + a_5H + a_6D + a_7W + A + I + t.$$

Four values of ΔW were measured for each individual. For ΔW in a particular direction, we used data for O_2–O_4, W, and A in the corresponding direction (e.g., for ΔW_N measured on the north side of a crown, we used O_2 calculated on the north side). In fitting the model, we pooled data from the thinned and intact plots.

We selected models for the model that best expressed the patterns in the data using the Akaike information criterion (AIC). The candidate models were the full model and its reduced models in which the explanatory variables were a subset of those for the full model.

We analyzed ΔL using a similar method. The full model for ΔL was

$$\Delta L = b_0 + b_1O_1 + b_2Mo_2 + b_3Mo_3 + b_4Mo_4 + b_5D + b_6L + b_7Mw + I + t,$$

where Mo_2, Mo_3, Mo_4, and Mw are the averages of four values of O_2, O_3, O_4, and W, respectively. The best model was selected using the AIC.

Results

The best model for ΔW contained O_1, O_4, H, D, W, A, and I. The best model for ΔL contained O_1, D, L, Mw, and I. The light availability on the side surface of the crown was important in determining horizontal crown expansion, whereas the light availability on the top of the crown determined vertical crown growth. The parameters for O_1 and O_4 (i.e., b_1, a_3, and a_4, respectively) were all positive, indicating that crowns expanded more rapidly as light availability increased.

Discussion

Because crown development determines important ecological processes within forests, numerous observations have been made on crown development using certain crown dimensions (e.g., Osada, 2006; Remphrey and Pearn, 2006; Takahashi and Rustandi, 2006). We observed crown development for 8 years and succeeded in modeling crown development in relation to the localized light environment. The models obtained can be used to predict crown development for forest management purposes.

The results demonstrated that crown development is autonomous to some extent. The selected model for ΔW showed that horizontal crown expansion in a certain direction is dependent on the light availability on the side surface of crown in that direction. The selected model for ΔL indicated that vertical crown growth is dependent on the light availability at the top of the crown. The autonomous response of crowns to the heterogeneous light conditions around them causes an asymmetric crown shape (Sorrensen-Cothern et al., 1993; Takanaka, 1994). Plants can capture more light via plastic adjustment of their foliage distribution to match the heterogeneous light availability (Umeki, 1995). At the stand or forest level, the morphological plasticity in crown shape increases light interception and biomass production (Umeki, 1997).

Future research on the crown expansion should address: 1) can more realistic calculation of the amount of intercepted light that takes sun tracks into consideration explain crown expansion better?, 2) can more realistic representation of crown shape improve the model fitting?, and 3) if we divide the growth process into two parts: matter production and growth allocation, can it explain crown expansion better?

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