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High frequency of discontinuous rings in evergreen and deciduous hardwood species in a temperate forest

Yuko Yasuda[a,*], Yasuhiro Utsumi[b], Tsutomu Enoki[c], Shinya Koga[c]

[a] Kyushu University Graduate School, Bioresource Environmental Science Institute, Hakozaki 6-10-1, Higashi-ku, Fukuoka 812-8581, Japan
[b] Kyushu University, Ashoro Research Forest, Kita 5-jyo 185, Ashoro-cho, Ashoro-gun, Hokkaido 089-3705, Japan
[c] Kyushu University, Kasuya Research Forest, Tsubakuro 394, Sasaguri-cho, Kasuya-gun, Fukuoka 811-2415, Japan

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ABSTRACT

Tree age derived from annual-ring counts provides fundamental information on forest stands and individual trees in temperate forests. However, discontinuous growth in the trunk may cause inaccuracies in annual-ring counts, and the effect of radial growth rate and interspecific differences on discontinuous ring formation have not been evaluated in the same forest stand. We investigated the occurrence of discontinuous rings at the base of 435 tree trunk disks of 16 evergreen and 15 deciduous hardwood tree species growing in a temperate forest of Japan. The effects of tree age and radial growth rate on frequency of discontinuous rings and their interspecific differences were evaluated by a generalized linear mixed-effect model. Discontinuous rings were observed in 29 of the 31 species in 330 individuals, which is about 75% of the total number of individuals examined. The number of discontinuous rings proportionally decreased with the growth rate and increased with the tree age. On the other hand, the effects of the growth rate were different among species. The majority of species at the study site contained frequent discontinuous rings in the trunk base. Annual-ring counts from a single core would lead to underestimation of tree ages in this case. Stem disks or increment cores taken in multiple directions at ground level would be useful for accurate estimation of tree age in temperate hardwood forests.

1. Introduction

A tree forms an annual growth ring in temperate forests through seasonal xylem cell differentiation from the cambium. Consequently, the annual ring number at the root collar approximates the tree age. Tree age derived from annual-ring counts is fundamental information to estimate the date of origin of trees and forest stands and to assess forest age structure (Borges Silva et al., 2017; Waring and O'Hara, 2006). Annual-ring counts are also frequently used in retrospective studies of forest stand dynamics (Piovesan et al., 2005) and disturbance history (Bergeron et al., 2004) by crossdating. Ring width fluctuates in response to disturbance (Canham, 1988; Henry and Swan, 1974; Heyerdahl et al., 2012; Koprowski and Duncker, 2012; Lorimer and Frelich, 1989; Piovesan et al., 2005; Rozas, 2003; Swetnam and Lynch, 1989) and climatic variability (Hasenauer et al., 1999; Koprowski and Duncker, 2012; Worbes, 1999). Radial growth changes are indicators of tree health (Innes, 1993; Cherubini et al., 2002) and activity (Vitali et al., 2016). Quantitative assessment of forest structure and stand-development patterns relies upon accurate ring count and ring width data.

Ring count data with increment cores are useful for evaluating individual tree growth and environmental changes because increment cores taken at either breast height or the base of stems are assumed to show a series of annual rings for every year the tree has been alive (Waring and O'Hara, 2006). Trees do not always lay down a continuous sheath of xylem over the entire stem, leading to 'absent (or 'missing') and 'discontinuous' (or 'partial') growth rings, especially under conditions of environmental stress (Bormann, 1965; Fritts, 1976; Fritz, 1940; Fritz and Averill, 1924; Kramer and Kozlowski, 1979; Lorimer et al., 1999). A discontinuous ring is a growth ring that is not present continuously around the stem (Committee on Nomenclature and International Association of Wood Anatomists, 1964). The formation of discontinuous rings is thought to be caused by partial suppression of radial growth for more than one year (Bormann, 1965; Fritts, 1976; Kohyama, 1980; Lorimer et al., 1999; Turberville and Hough, 1939; Waring and O'Hara, 2006; Yasuda et al., 2018). Absent rings and discontinuous rings have been reported in some tree species (Brown and Swetnam, 1994; Fritz and Averill, 1924; LaMarche and Harlan, 1973;

* Corresponding author.
E-mail addresses: yyasuda0211@gmail.com (Y. Yasuda), utsumi@forest.kyushu-u.ac.jp (Y. Utsumi), enoki@forest.kyushu-u.ac.jp (T. Enoki), skoga@forest.kyushu-u.ac.jp (S. Koga).

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Schulman, 1940).

In humid regions with dense temperate forests, discontinuous rings and absent rings are more frequent in suppressed trees than in dominant canopy trees (Bormann, 1965; Lorimer et al., 1999; Turberville and Hough, 1939). Discontinuous and absent rings can occur in trees in response to drought (Fritts, 1976), defoliation (Krause & Morin, 1995), pollution damage (Athari & Kramer 1983), shading (Bormann, 1965; Roberts, 1994), and in cold seasons at the tree line (Colenutt & Luckman, 1991). The discontinuous and absent rings potentially cause inaccurate ring counting in increment core analysis. Many increment core studies use a single core to elucidate the age of an individual tree at one height (Bergin and Kimberley, 2012; Heyerdahl et al., 2012; Koprowski and Duncker, 2012; Myers, 1963; Rozas, 2003; Piovesan et al., 2005; Takaoka, 1993). If discontinuous rings are present in a core sample, an accurate number and position of discontinuous rings cannot be determined without dendrochronological correction (Lorimer et al., 1999) or knowledge of the forest stand history (Takaoka, 1993). In addition, an increment core might fail to reach the chronological center of the stem containing the pith. The chronological center is not always located in the geometric center of the trunk, because the trunk may be asymmetrical in cross-section owing to eccentric growth. Duncan (1989) reported that the mean percentage error from 84 cores that passed within 50 mm of the chronological center was ± 35% in *Dacrycarpus dacrydioides* de Laub. The other potential error arises from the core sampling height. Previous studies using two cores taken at different trunk heights suggest that tree rings are not formed regularly every year throughout the trunk, but entire tree rings may be absent or only partially developed under the suppressed condition (Cherubini et al., 2002; Wong and Lertzman, 2001). Yasuda et al. (2018) also reported partial absence of annual rings in the middle and lower sections of trunks of *Abies sachalinensis* Mast. grown under shade.

Previous studies suggest that ring anomalies can lead to errors in analyses of stand dynamics, growth rate, site index, and tree vigor that are reliant on increment cores (Brown and Swetnam, 1994; Fritz, 1940; Fritz and Averill, 1924; Takaoka, 1993; Wong and Lertzman, 2001). Increment core sampling may not be a robust approach to obtain accurate age data without cross dating because of high variability in annual ring counts and width within a species in the same stand in some cases (Waring and O'Hara, 2006). The occurrence of ring anomalies in trees of temperate forests is occasionally reported (Lorimer et al., 1999, Niklasson, 2002), but direct detection of discontinuous rings requires more than one increment core taken in different radial directions from the pith to the bark in an individual tree or, preferably, a complete disk of the trunk. However, disk sampling involves destructive tree felling and time-consuming analysis of stem disks. Therefore, relatively few studies have evaluated annual ring data using disks (Fraver et al., 2011; Krause & Morin, 1995, Lorimer et al., 1999; Norton et al., 1987; Waring and O'Hara, 2006). These previous studies analyzed a single species, of which the majority were conifers (Bergin and Kimberley, 2012; Cherubini et al., 1998; Duncan, 1989; Niklasson, 2002; Norton et al., 1987; Waring and O'Hara, 2006). Few studies have investigated ring anomalies in deciduous (Lorimer et al., 1999, Takaoka, 1993) and evergreen hardwood species (Norton et al., 1987). To the best of our knowledge, the occurrence of discontinuous rings in evergreen and deciduous hardwood species in the same forest stand has not been evaluated previously.

In this study, a temperate secondary forest composed of both evergreen and deciduous hardwood species was clear cut, and the frequency of discontinuous annual rings was analyzed statistically using 435 trunk base disks. In addition, the interspecific differences and the effect of growth rate on the frequency of discontinuous rings were evaluated.

2. Materials and methods

2.1. Study site and plot measurement

The study site was in the Kasuya Research Forest, Kyushu University (130°31′E, 33°38′N), which was established in 1922. The altitude of the study site is 75–90 m above sea level. The study site was established on a hill slope facing south to south-east. The slope is around 20° with maximum 30°. The soil is forest brown soil, and the soil texture is silty clay. The bedrock consists of Tertiary sandstone and mudstone. Annual precipitation is 1790 mm/year, and the annual average temperature is 16 °C (DEIMS-SDR). Monthly maximum precipitation was 279 mm in July and monthly minimum precipitation was 68 mm in January from 2008 to 2017 with no dry season. The study site has no history of forest management, including clear-cutting, since its establishment. Most of the natural forest area consist of warm-temperate evergreen hardwood species, such as *Quercus glauca* Thunb., *Castanopsis sieboldii* Hatus., *Machilus thunbergii* Siebold et Zucc. and *Morella rubra* Lour., and deciduous hardwood species, such as *Carpinus tschonoskii* Maxim., *Quercus serrata* Murray and *Castanea crenata* Siebold et Zucc.

In January 2014, 30 quadrats of 10 m × 10 m were established at the study site. The diameter at breast height and the height of trees ≥15 cm in circumference at the trunk base were measured. The number of trees, average diameter at breast height, and average tree height were calculated from the survey data.

2.2. Tree ring analysis

In February 2014, all trees in the quadrats were cut down and disks of 10 cm thickness without heartwood rot were taken from the stem at 20 cm above ground level for 435 trees ≥15 cm in circumference at the trunk base. After the sampled disks were dried for one month, the disks were smoothed with a belt sander (Bergin and Kimberley, 2012) using different grit sizes (P60, P120 and P240; Makita, Japan, Yasuda et al., 2018). Two radial directions from the pith to the bark separated by more than 90° on each disk were determined. The first radius was selected at the maximum radial length on the disk with no decay from the pith to bark, and the second radius was placed on the second largest radial length 90° or more away from the first radius with no decay. For disks in which annual-ring identification was difficult, the surface was further shaped with a razor blade. The number of annual rings on the disk was counted using a loupe and a stereomicroscope. From the two measured directions, the difference between the maximum number of annual rings (MANR) and the smaller number of annual rings (MINR) was taken to be the number of discontinuous rings (NDR). Radial growth rate (GR) obtained by dividing DBH/2 by MANR. Tree ring data were not crossdated because most of the studied species grew under suppressed condition and contained significant numbers of discontinuous ring.

2.3. Stand discontinuous-ring variability

To evaluate the factors affecting NDR, a generalized linear mixed-effects model was constructed as the full model:

$$\mathrm{NDR} = a_0 + b_{0i} + (a_1 + b_{1i})*\mathrm{MANR} + (a_2 + b_{2i})*\mathrm{GR}$$

where MANR and GR are covariates. Regression parameters, intercepts, and coefficients are expressed as a_0, a_1, and a_2, respectively. We took into account differences between tree species (SP) as random effects for the intercept [b_0] and the slope [b_1 and b_2] in the models, and i represents the parameter of each species. The response variable (NDR) was assumed to follow the Poisson distribution. The log link function was used. We chose GR because the discontinuous rings would be formed generally when radial growth decreased (Lorimer et al., 1999, Yasuda et al., 2018). We assumed NDR would increase as MANR increased. We used the tree species as a random effect, because several