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NOTE

Assessing intra-annual density fluctuations across and along white pine stems

Elise W. Miller, Tim Rademacher, Patrick Fonti, Bijan Seyednasrollah, and Andrew D. Richardson

Abstract: Intra-annual density fluctuations (IADFs) are triggered by environmental cues, but whether they are distributed uniformly throughout the stem is not well documented. The spatial distribution of IADFs could help us understand variations in cambial sensitivity to environmental cues throughout the tree. We investigate how IADF distribution varies radially, longitudinally, and circumferentially within white pine (*Pinus strobus* L.) stems. We took wood samples at breast height, near branches, and at the top of the trees. We identified IADFs visually and measured their radial position within a ring as well as their circumferential arc in cross-sections. Intra-annual density fluctuations occurred in 22.2% of rings. The radial position of IADFs within a ring was remarkably consistent at roughly 80% of the total annual radial increment across heights, trees, and years of formation. The main factors affecting the likelihood of IADF occurrence were ring width, year of formation, and the interaction between the two. Being near branches or at the top of the tree slightly increased the probability of occurrence. Though the sample size was not large enough to provide conclusive results about the circumferential distribution of IADFs, our data suggest that the circumferential arc of the IADFs might be conserved throughout the stem.

Key words: carbon, climate, false rings, IADFs, white pine, wood density, wood anatomy, wood formation, xylogenesis.

Résumé : Les fluctuations intra-annuelles de densité (FIAD) sont déclenchées par des signaux environnementaux, mais leur distribution uniforme dans la tige n'est pas bien documentée. La distribution spatiale des FIAD pourrait aider les chercheurs à comprendre les variations de la sensibilité du cambium aux signaux environnementaux à travers l'arbre. Les auteurs examinent comment la distribution des FIAD varie radialement, longitudinalement et de manière circonférentielle dans les tiges de pin blanc (*Pinus strobus* L.). Ils ont prélevé des échantillons de bois à hauteur de poitrine, près des branches et à la cime des arbres. Ils ont identifié visuellement les FIAD et mesuré leur position radiale à l'intérieur d'un anneau ainsi que leur arc circonférentiel dans les coupes transversales. Les FIAD étaient présentes dans 22,2 % des cernes. La position radiale des FIAD à l'intérieur d'un anneau était remarquablement constante à environ 80 % de l'incrément radial annuel total à travers les hauteurs, les arbres et les années de formation. Les principaux facteurs affectant la probabilité d'apparition de FIAD étaient la largeur du cerne, l'année de formation et l'interaction entre les deux. Le fait d'être près des branches ou au sommet de l'arbre augmentait légèrement la probabilité d'apparition. La taille de l'échantillon n'était pas assez importante pour fournir des résultats concluants sur la distribution circonférentielle des FIAD, bien que les données suggèrent que l'arc circonférentiel des FIAD pourrait être conservé tout au long de la tige. [Traduit par la Rédaction]

Mots-clés : carbone, climat, faux cernes, FIAD, pin blanc, densité du bois, anatomie du bois, formation du bois, xylogenèse.

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Introduction

Annual wood growth rings, which are formed in seasonal climates, illustrate how wood formation varies inter- and intra-annually in trees. In temperate and boreal conifers, radial growth generally transitions from relatively large thin-walled cells known as earlywood, to relatively small thick-walled cells known as latewood, throughout the growing season (Björklund et al. 2019). Thus, in a typical conifer growth ring there is usually an increase in the density profile throughout the growing season with maximum density occurring close to the end of the ring. Fluctuations from this characteristic density profile can occur if cambial activity slows down or even stops and then resumes normal growth within that same growing season (De Micco et al. 2016). These fluctuations are referred to as false rings, double rings, or intra-annual density fluctuations (IADFs). Intra-annual density fluctuations are usually induced by external disturbances (Fritts 1976) such as drought, air pollution, floods, extreme temperatures, sudden frosts, and (or) defoliation (Marchand and Filion 2012 and references within).

Research has focused on the drivers of IADFs at breast height (Campelo et al. 2007*a*; Marchand and Filion 2012; De Micco et al. 2016; Zalloni et al. 2016), but few studies have examined the spatial occurrence of IADFs within stems. It is known that the position of IADFs within a growth ring may vary and can occur either in the earlywood or the latewood (Campelo et al. 2007*a*; Battipaglia et al. 2016), which can be used to roughly date IADFs (Campelo et al. 2007*b*; De Micco et al. 2014). Whether the radial position of IADFs in growth rings is consistent among different trees of the same stand or whether its occurrence differs along the longitudinal and tangential stem axis remain open questions. Because environmental cues such as a summer drought and (or) autumn precipitation (Campelo et al. 2007*b*; Hoffer and Tardif 2009; Novak et al. 2013) can trigger IADFs and because the trees in a stand are often experiencing triggers concurrently (Copenheaver et al. 2006), the radial position of IADFs among trees in a stand is likely similar during the same year of formation. However, in different years, the drivers of IADFs may not always occur at the same time during the growing season leading to between-year variations in the radial position of IADFs in the same individual.

Beyond the position within a ring, there is little information about the distribution of IADFs along and around the stem. However, since other wood anatomical features such as missing rings have been found not to be distributed homogeneously along and around the stem of trees (Novak et al. 2011), it is possible that IADF distribution may also not be evenly spatially distributed. Such differences in their distribution may result from variations in cambial sensitivity to environmental cues throughout the stem, which could be used to better understand wood growth.

There are several potential factors that might influence the spatial distribution of IADFs in the stem. Previous studies have found that ring width, which can be used as an indicator of vigor, is strongly correlated with IADF formation, and trees with wider rings were more likely to have IADFs (Vogel et al. 2001; Campelo et al. 2013; Novak et al. 2013; Zalloni et al. 2016). It has been argued that areas of increased cambial activity such as near branches affect the production of IADFs (Fritts 1976). One study on *Quercus ilex* L. found that IADFs were equally likely to be formed throughout the height of the tree (Campelo et al. 2007*b*). In contrast, a study on a single Ponderosa pine observed a greater tendency for IADFs in the upper stem, but this relationship was only found in the inner rings (Schulman and Baldwin 1939). Other studies have also found that IADFs may not occur uniformly throughout the longitudinal axis of a tree (Copenheaver et al. 2006; Hoffer and Tardif 2009). Variations in the distribution of IADFs along the stem may be related to, or even controlled by, differences in cell wall chemical composition in cellulose content and gene expression along the stem (Paiva et al. 2008). However, no study to our knowledge has looked at the circumferential extent of IADFs and how this varies with height. It is possible that IADFs could conserve the total circumferential distance with height, thus spanning a smaller arc towards the bottom of the tree due to the stem's taper; however, the circumferential arc of the IADFs might also be conserved, which would lead to an increase in circumferential distance towards the bottom of the tree.

To address these questions about intra-tree spatial cambial sensitivity, we studied the radial, longitudinal, and circumferential distribution of IADFs in white pine (*Pinus strobus* L.). We hypothesize the following: (H1) that the relative position of IADFs within the ring is conserved across different trees for the same year, but not across years for the same tree; (H2) that IADFs are more likely to occur in larger rings, higher up the tree, and near branches; (H3) and that the circumferential arc of an IADF is not conserved along the stem.

Materials and methods

Sample site and preparation

To study the formation of IADFs, we sampled 41 white pines at Harvard Forest in Petersham, Massachusetts (42.50°N latitude, 72.22°W longitude; roughly 340 m a.s.l.), which is a temperate mesic environment on well-draining stony loam soils. The mean annual precipitation of 1170 $\pm$ 193 mm ($\mu \pm \sigma$) is evenly spread across the seasons, and the mean annual temperature is 8.0 $\pm$ 0.8 °C ($\mu \pm \sigma$) (Boose and Gould 2019). Temperatures range from a mean July temperature of 20 °C to a mean January temperature of −7 °C.

For sample collection, we chose white pine trees that had a single straight bole for at least four meters above the root collar and showed no obvious signs of recent damage. The trees naturally regenerated after a clear-cut in 1990 and ranged from 15 years to 26 years of cambial age at breast height, 9 m to 14 m in height, and between 15 cm to 25 cm in diameter at breast height. All trees

Fig. 1. (*a*) Schematic of the average tree indicating the three spatial dimensions (e.g., longitudinal, circumferential, and radial) and our sampling locations (breast height, near branch, and top of the tree). (*b*) Examples of intra-annual density fluctuations (marked with red dashed lines in the right half of each image) in scans of white pine. (*c*–*e*) Show the sample size (grey-dashed line) and the percentage of annual rings with intra-annual density fluctuations for each year in growth sections from (*c*) towards the top of the tree (green), (*d*) near branches (dark blue), and (*e*) from breast height (light blue), respectively. [Colour online.]

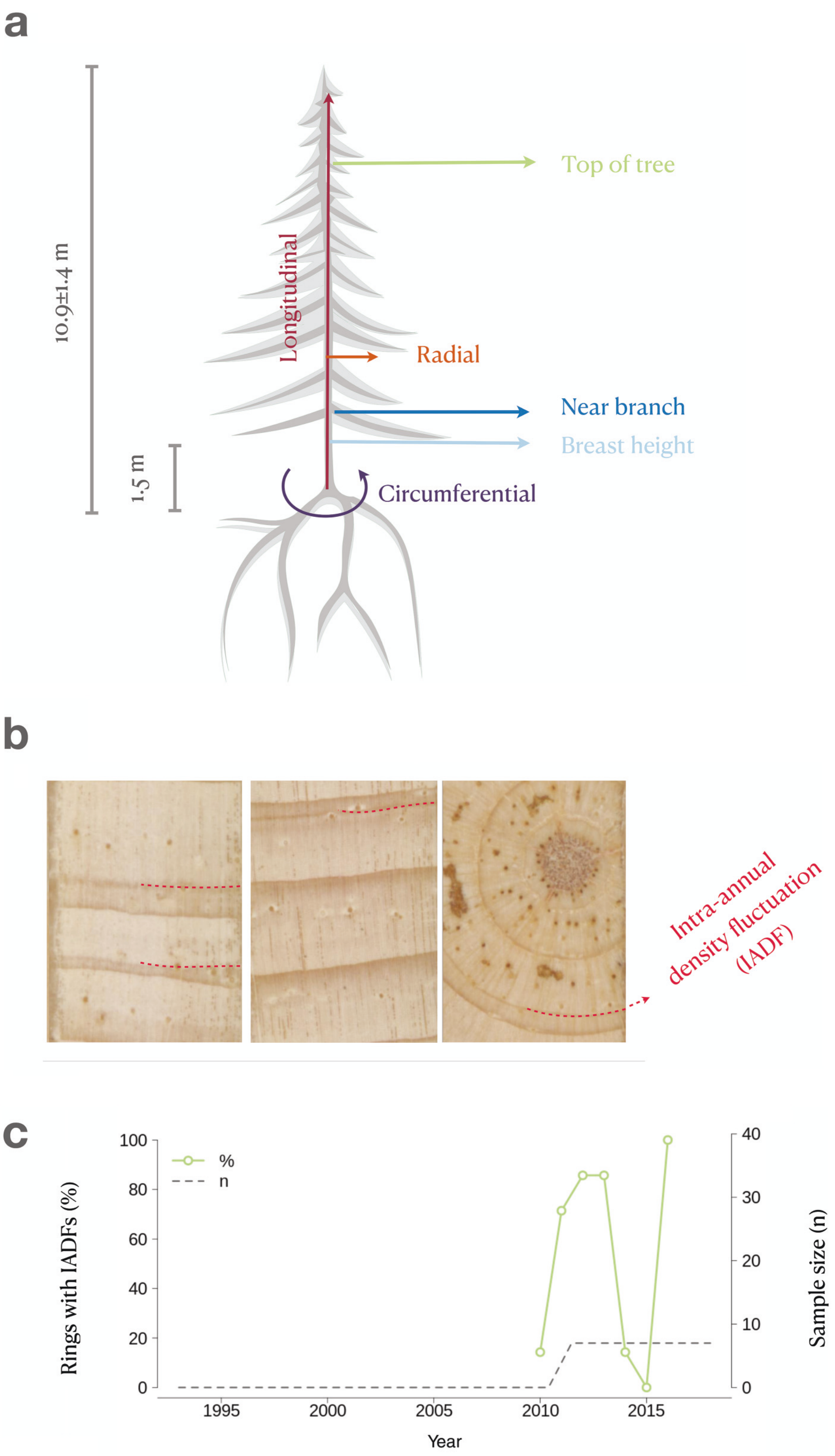
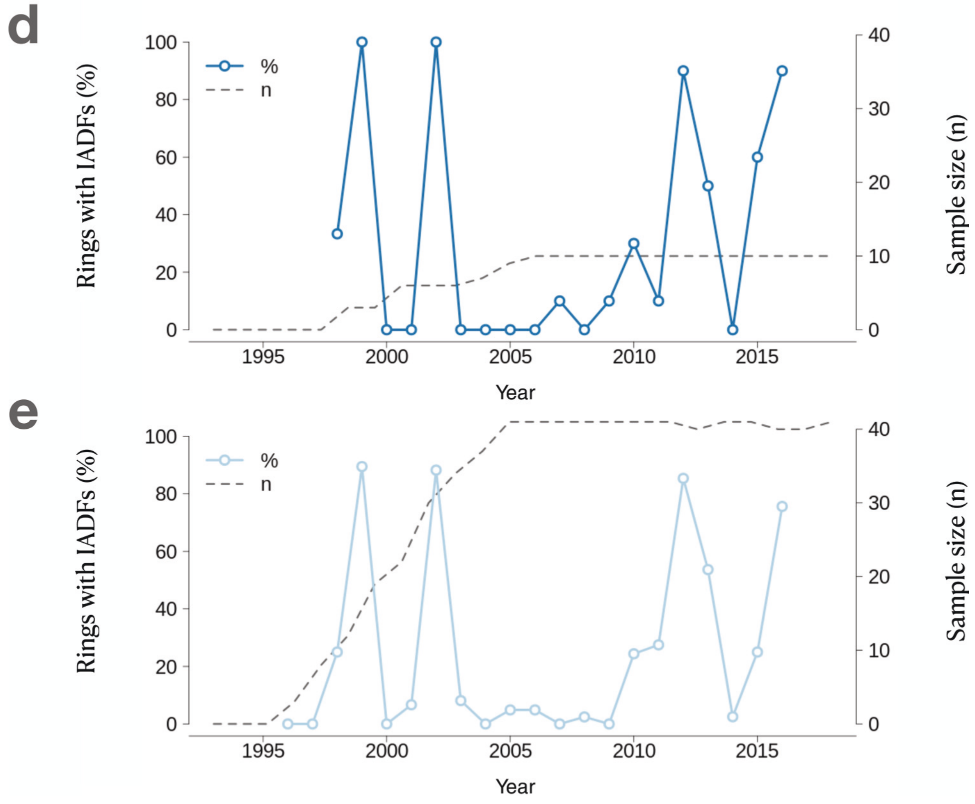


Fig. 1 (*concluded*).



occupied a codominant canopy position, and their surroundings did not show signs of recent disturbance. We sampled in June and July 2019 and excluded the 2017, 2018, and 2019 growth increments because some of the trees had been girdled and compressed in 2017 to alter their radial growth for another experiment (see Rademacher et al. 2021*a* for details).

We collected increment cores from all 41 trees at breast height (ca. 1.5 m) using a 5.1 mm three-threaded Haglöf standard increment borer (Långsele, Sweden). A random subset of 10 trees was cored near the next branch whorl above breast height. All the increment cores contained the entire diameter, which gave us two opposing series of radial growth. To study the longitudinal and circumferential distribution of IADFs, we cut down a subset of seven trees (not overlapping with the subset of 10 trees that were cored near branches). We chose trees that had succumbed to the girdling and compression treatments (Rademacher et al. 2021*a*) after the 2017 growing season, but excluded growth that had occurred after the treatments. For these seven trees, we cut cross-sections at breast height and in the middle of a stem section that grew towards the top of the tree (Fig. 1*a*). To balance increasingly fewer rings but larger rings towards the top of the tree, we settled on the internode formed in the 2010 growing season, providing seven annual rings. After mounting the cores, we sanded the cores and cross-sections with incrementally finer sandpaper (e.g., 80 grit to 8000 grit) and scanned them using an Epson Perfection V600 Photo Scanner (Long Beach, California, USA) at 2400 dpi.

Identification and measurement of ring widths and IADF position

After cross dating the cores and cross-sections, we visually recorded the presence of IADFs in each growth ring. We identified IADFs as tangential bands of smaller cells with thicker walls that are surrounded by larger, thinner-walled cells, which are visible as darker bands within the growth increment (see Fig. 1*b*). For measurements of ring width and the position of the IADFs within the ring, we used the open-source Wood Image and Analysis Database (https://wiad.science) platform (Rademacher et al. 2021*b*; Seyednasrollah et al. 2021). We used the open-source GNU Image Manipulation Program version 2.8 (https://www.gimp.org/) to measure the circumferential arc of the IADFs in images of cross-sections from breast height and the top of the tree.

Statistical analyses

To test H1, whether the relative position of IADFs within the ring differed little across trees for the same year, but more across years for the same tree, we fitted the following varying intercept model to the standardized relative position of each IADF within each growth ring (i.e., *z* score of the percentage of the ring width is *relPos*).

$$(1)\qquad relPos \sim \text{normal}(\mu_r, \sigma_r)$$

$$(2)\qquad \mu_r = \alpha_y + \alpha_t$$

Given the centered nature of the response variable, we used a relatively uninformative wide normal distribution with a standard deviation of 0.5 as priors for α_y and α_t and an exponential function with exponent 1 as prior for σ_r.

To test H2, whether the probability of occurrence of an IADF (*P*(*IADF*)) changed depending on ring width and the sampling height along the stem (i.e., breast height, top of the tree, and near a branch), we fit a logistic regression model to predict the probability of occurrence of IADFs. The complete model took the following form:

$$(3)\qquad P(IADF) \sim \text{binomial}(1, p)$$

$$(4)\qquad \text{logit}(p) = \alpha_y + \alpha_{BRA} + \alpha_{TOP} + \beta_1 rw_{y,t} + \beta_2 rw_{y,t}y$$

where α_{BRA} and α_{TOP} represent the effect of being near a branch or towards the top of the tree, respectively. Given the strong prevalence of IADFs in certain years, we decided to include year of formation as varying intercepts (α_y) in the model. Additionally, we included ring width ($rw_{y,t}$) of tree t formed during year y, because ring width is a known influence on IADF occurrence (Vogel et al. 2001; Campelo et al. 2013; Novak et al. 2013; Zalloni et al. 2016). We included the interaction of year of formation and ring width ($rw_{y,t}y$), to account for a potential interaction between years with triggering events and tree vigour. While the complete model is based on biological knowledge, we also tested simpler models based on these variables. For each model, we used normal priors with a mean of 0 and a standard deviation of 0.3 for slope parameters (i.e., β) and 0.9 to 1.5 for intercepts (i.e., α), depending on the number of intercepts. The standard deviation for intercept priors was chosen based on prior predictive sampling to create a combined flat prior in the sampled log-odds space.

To test H3, whether the circumferential arc of the IADFs differed substantially at the top of the tree versus at breast height, we fitted a von Mises distribution to the circumferential arc (*arc*) or a normal distribution to its length (*len*) at breast height versus at the top of the tree. For example, the model for the circumferential arc is as follows:

$$(5)\qquad arc \sim \text{von Mises}(\mu_a, \kappa_a)$$

$$(6)\qquad len \sim \text{normal}(\mu_a, \sigma_a)$$

$$(7)\qquad \mu_a = \alpha_y + \beta_1 TOP$$

where α_y varies with year of formation and β_1 captures the effect of being near the top of the tree. We also tested a non-varying intercept (α_0) and an intercept to account for between-tree variation (α_t). The results were qualitatively robust across all three models; thus, we will report the model described in eqs. 5 and 6, which minimized the widely applicable information criterion. Priors for α_y and β_1 were set to relatively uninformative wide normal distributions with mean 0 and standard deviation of 10, while the prior for σ_a and κ_a were set to an exponential function with exponent 1. All distributions were estimated using four chains of the Hamiltonian Monte Carlo algorithm as implemented through the ulam function of the rethinking package version 2.13 (McElreath 2020) or the stan function of the rstan package version 2.21 (Stan Development Team 2020) in R version 4.1.0 (R Core Team 2020). Sufficient exploration of the parameter space by the chains was visually evaluated using rank histograms and trace plots. Below we report posterior means with their 90% credible intervals. All code and data to reproduce the results is publicly available on the Harvard Forest Data Archives (Miller and Rademacher 2020).

Results

Intra-annual density fluctuations were surprisingly common, occurring in 22.2% of rings ($n = 1804$). All 41 trees had at least one IADF. A small subset of nine rings even contained two IADFs. Across years, only rings formed in the year 2000 and 2004 showed no IADFs at all. In the average year, only 4% of the annual rings at breast height had an IADF, but IADFs occurred in 71% of rings in five specific years: 1999, 2002, 2012, 2013, and 2016 (Figs. 1*c*–1*e*). Surprisingly, the relative radial position of IADFs was very consistent at about 80% of the fully formed ring with little between-year (Fig. 2*a*) and between-tree variation (Fig. 2*b*). For three years each, IADFs formed slightly earlier (2011, 2013, 2016) or later (1998, 2002, 2010), but even in those extreme years, the posterior mean of relative positions only ranged from 73.9% to 85.9% of the formed ring. Five trees (i.e., 11, 19, 23, 28, and 36) also tended to form IADFs slightly earlier, whereas no tree formed IADFs distinguishably later in the ring formation process with tree 8 and 27 having the largest posterior mean relative position at roughly 85% of the formed ring (Fig. 2*b*). Overall, this evidence supports our hypothesis (H1) that IADFs tend to occur at similar relative positions in trees of the same stand in any particular year, but the evidence does not support our hypothesis that the relative position does vary substantially between years in the same tree.

Year of formation and ring width were also important factors when evaluating the probability of IADF occurrence. The same five years highlighted above (i.e., 1999, 2002, 2012, 2013, and 2016) were the only years for which the intercept of the logistic regression was reliably positive (based on the 90% credible interval of their posterior distribution), suggesting that these years and only these years increase the probability of occurrence (Fig. 3).

The relationship between ring width and probability of occurrence depends on the exact model structure. If we only include ring width as a predictor, the probability of occurrence of IADFs decreases by 7.5% (5.6% to 9.3%) when

Fig. 2. The 90% credible interval and posterior mean radial position of intra-annual density fluctuations as a percentage of ring width (*a*) during different years (*b*) and among different trees in the same year. The gray bars indicate the overall posterior mean position and one standard error. [Colour online.]

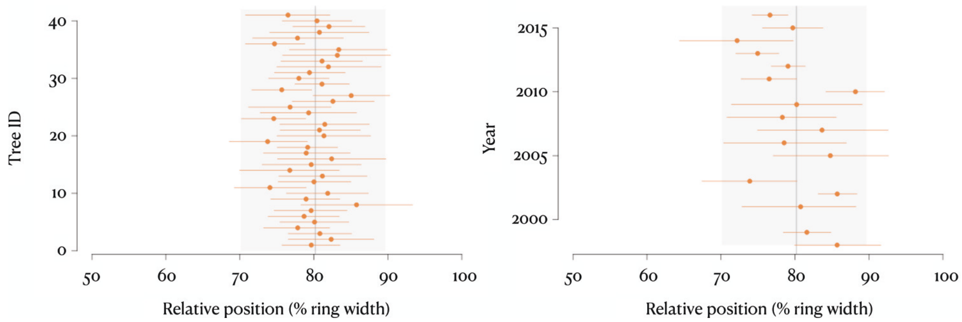
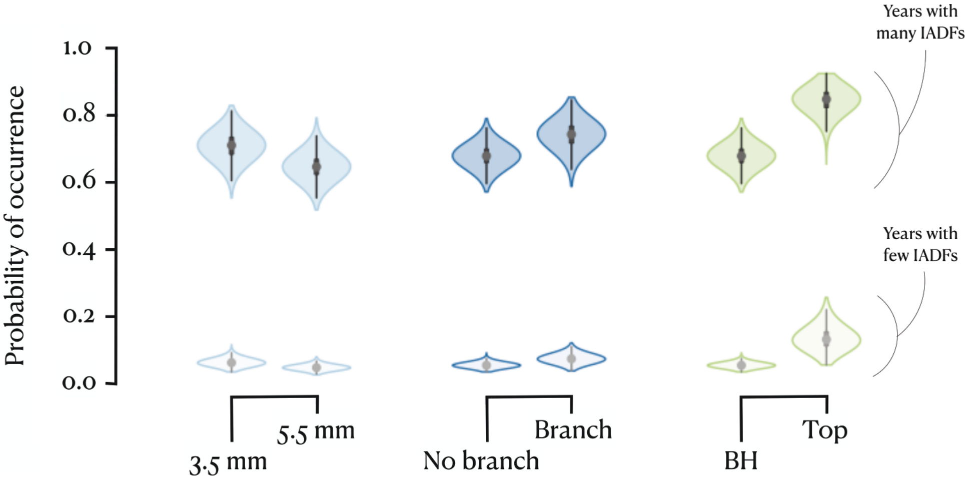


Fig. 3. Violin plots of the probability of occurrence of intra-annual density fluctuations during years with many IADFs (i.e., 1999, 2002, 2012, 2013, 2016; darker plots at the top) and few IADFs (i.e., that is all remaining years; lighter plots at the bottom) for (*a*) rings narrower than average (3.5 mm) and rings wider than average (5.5 mm), (*b*) for samples taken at breast height or near a branch, and (*c*) samples taken at breast height or towards the top of the tree. [Colour online.]



ring width increases from slightly below average at 3.5 mm to slightly above average at 5.5 mm ($\mu_{rw} \pm \sigma_{rw} \approx$ 4.5 mm ± 2.1 mm). When a varying intercept for the between-year variations is added to ring width as a predictor, the probability of occurrence of IADFs instead increases by 3.8% (0.8% to 6.6%) when ring width increases from 3.5 mm to 5.5 mm in IADF-prone years and by 1.1% (0.2% to 1.9%) in years with few IADFs. If an interaction term between ring width and year is added on top, the overall effect when going from a 3.5 mm to a 5.5 mm wide ring reverses once more by decreasing the probability of occurrence by 7.25% (1.3% to 13.3%) and 2.0% (0.3% to 3.8%) in years with many and few IADFs, respectively. This holds true whether we sample from the data at breast height or sample from all data.

Being higher up in the tree or near a branch whorl was estimated to increase the probability of IADF occurrence by 16.7% (9.8% to 23.3%) and 6.3% (0.1% to 12.2%) in years with many IADFs and by 8.1% (3.5% to 13.8%) and 1.9% (0.0% to 4.0%) in years with few or no IADFs, respectively (Fig. 3). While the model based on only ring width, year of formation, and their interaction did minimize the widely applicable information criterion (best choice in 49% of cases), adding being at the top of the tree still improved the model in 35% of cases. Including being near a branch was able to capture the information better in 8% of cases, and the additional complexity of integrating both (i.e., being near the top of the tree and near a branch) only optimized the information captured in 7% of cases.

Mean arcs were 100° larger towards the top of trees, but the mean circumferential arc of the IADFs was almost identical at 10.1 mm. Unfortunately, we only had measurements for 64 arcs in total, which was insufficient to obtain reliable posterior distribution for the arc and its length. While these differences were also apparent in the posterior, supporting our hypothesis (H3) that the circumferential arc of the IADFs is not conserved along the stem, prior predictive sampling suggests that between 100 and 1000 samples would be needed to reliably estimate even such a strong effect on the arc. Given the variability of the circumferential arc of the IADF measurements, even more samples might be needed if conditioning for potential confounds such as year of formation, tree ID, and ring width is necessary.

Discussion

In recent years, IADFs have been used to study how wood formation and tree growth respond to environmental factors. In fact, the majority of the research on IADFs focuses on their drivers (Hoffer and Tardif 2009; Marchand and Filion 2012; Zalloni et al. 2016), with fewer studies having investigated how IADFs form and how their resulting distribution varies along the stem. Because previous studies have found that there are differences in wood properties such as cambial cell division and cell wall thickness in conifers (Cato et al. 2006), the spatial distribution of IADFs may provide information on how cambial sensitivity to environmental triggers varies along the stem. Here, we specifically looked at the radial, longitudinal, and circumferential distribution of IADFs within the stem of white pine trees for the first time.

We found that IADFs occurred in 22.2% of formed rings. This number falls within the wide range of observations reported in other studies that found 34% percent of rings had IADFs in the latewood (Campelo et al. 2015) and 0.3% to 33% of rings had IADFs depending on the site (Novak et al. 2013). We found strong between-year variation in the probability of IADFs with much larger numbers occurring during five specific years (1999, 2002, 2012, 2013, and 2016). While this is not the focus of our investigation, it is important to note that these years correspond to relatively dry summers at Harvard Forest (Supplementary Fig. S1[1]). This finding is supported by other studies, which have also found that dry summers can lead to IADF formation (Zhang et al. 2020).

We studied whether the radial position of IADFs varies between individuals in a stand and in rings formed in different years within the same individual tree (H1). The IADFs had a close to constant radial position throughout all trees in a stand during the same year (Fig. 2*b*). Because the trees in a stand are experiencing a trigger at the same time, this finding makes sense. Surprisingly, the IADFs had a remarkably constant position in the rings throughout all the years as well (Fig. 2*a*). One explanation is that the exogenous trigger of the IADFs, such as drought followed by precipitation (Campelo et al. 2007*b*), occurred roughly at the same time during the growing season (i.e., when growth rates started declining), but this seems unlikely. Alternatively, the underlying mechanisms determining the intra-annual transition in cell characteristics may only allow for an integration of IADFs during a particular stage of the transition (i.e., the change is stepwise rather than continuous) in our white pines, though this seems unlikely as well. This would imply that the sensitivity for IADF formation is especially high during one particular developmental stage in the studied ecosystem. However, our current models of wood formation (e.g., Cartenì et al. 2018) assume a continuous development of cell characteristics. These models do not currently include environmental dependencies though, which may introduce step changes. If the sensitivity is much higher at a particular developmental stage, then the relative position of the IADFs may depend on how much growth occurs before and (or) after the induced reduction or stoppage of growth. Thus, IADF relative position may be controlled by the tree's carbon supply rather than the actual timing of the trigger. Future studies should more closely investigate the climatic triggers of IADFs to ascertain the responsiveness of the cambium to environmental changes during various phenological phases.

We also studied how factors such as ring width, longitudinal distribution, and year of formation impacted the likelihood of IADF occurrence throughout the stem (H2). Year of formation and ring width were two of the most important criteria in determining the probability of IADF occurrence. Overall, narrower rings had more IADFs in our study, but in IADF-prone years, the rings with IADFs were wider than those without (Fig. 3*a*), which is in agreement with previous studies (Vogel et al. 2001; Campelo et al. 2013; Novak et al. 2013; Zalloni et al. 2016). Because IADFs often form during conditions that are unfavorable for radial growth (i.e., relatively dry periods, Supplementary Fig. S1[1]), rings with IADFs may be narrower than during the usual year. Comparatively, rings with IADFs that are formed in IADF-prone years may be relatively wider than rings without for several reasons. For narrower rings, cambial activity tends to start later and finish earlier (Rathgeber et al. 2011), so there is a shorter period to record climatic variability and for IADFs to form. Trees forming narrower rings may also be generally more stressed; thus, they could lack the reserves necessary to resume cambial activity after climate conditions are favorable again (Zalloni et al. 2016; Popkova et al. 2018). Alternatively, wider rings may be formed due to either a higher rate of cambial cell production (Rathgeber et al. 2011) or due to a longer growing season (Rossi et al. 2008), which would allow for the formation of more cells after the improvement of conditions and the development of IADFs.

We also studied whether being at the top of a tree impacted IADF formation. Although we found evidence that wood formed higher up the tree is more likely to have IADFs, the effect on the likelihood of occurrence was relatively small (Fig. 3). In large trees, strong gradients of water potential occur along the stem with areas higher up the tree experiencing lower water potentials (Hellkvist et al. 1974). This lower water potential decreases turgor pressure, which could lead to a pronounced decrease in

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[1] Supplementary data are available with the article at https://doi.org/10.1139/cjb-2021-0218.

cell enlargement (Hölttä et al. 2010; Wilkinson et al. 2015). Given the importance of turgor for growth (Peters et al. 2021), the subtle difference we observe in our trees may be more substantial in larger trees. Alternatively, gradients of auxin exist along the stem (Wodzicki 1978) and are known to influence wood formation (Uggla et al. 2001), which could also affect the likelihood of IADF formation along the stem.

Being near a branch only marginally increased the probability of occurrence, with the lower bound of the 90% credible interval still being very close to zero. To test this effect more thoroughly in the future, a larger sample size would be necessary.

The final aspect of spatial distribution of IADFs our study examined was the circumferential distribution. Despite the low sampling size, there was weak evidence that the arcs themselves are not conserved, but the length of the arc might be. Given similarly large variability of the circumferential arc such as in our data, 100 samples would be required at the very least. Other factors such as varying resource availability (light, water, etc.) might modulate any purely geometric variations of the arc with height, therefore further complicating the detection of height related effects. A study on longleaf pine found a higher proportion of thicker-walled cells on the northern side of trees (Eberhardt et al. 2018), suggesting that resource gradients in the stem can affect cambial activity. Because of this, IADFs may form predominantly on a particular side of the stem. However, most IADF studies only analyze the years when IADFs are present on opposite sides of a core (Campelo et al. 2007*a*), which suggests that IADFs may form around the entire stem at least at the base. Future studies could mark the cardinal direction on cross-sections to investigate this hypothesis or take samples across more than two heights.

Conclusion

Intra-annual density fluctuations were observed in all trees although some individuals were more or less prone to form them. We found that the radial position of IADFs was constant in trees throughout the same stand and, surprisingly, in individuals during different years. When studying the factors that increased the probability of IADF occurrence, year of formation, ring width, and their interaction were the most important criteria. However, being at the top of the tree or near a branch also slightly increased the probability of IADF occurrence along the stem. Our sample size was too small to draw any firm conclusions about the circumferential distribution of IADFs. Nonetheless, we have weak evidence suggesting that though the circumferential arc of the IADFs are not conserved along the stem, the length of the arc might be.

Competing interests

The authors declare there are no competing interests.

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Author contributions

E.M. and T.R. designed the study, collected, and analyzed the data. All authors interpreted the data. E.M. wrote the manuscript with help from T.R. T.R. generated the figures. T.R. and B.S. developed the Wood Image Analysis and Database. All authors provided feedback and approved submission.

Data availability

All data and code for this manuscript is publicly available. The raw data and code data can be found in the Harvard Forest archive at the following link: https://harvardforest1.fas.harvard.edu/exist/apps/datasets/showData.html?id=HF347. The code to generate all statistics and figures can be found at the following link: https://github.com/TTRademacher/densityAnomaliesInWhitePine.

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