RINGS OF COLLAPSED CELLS IN *PINUS RADIATA* STEMWOOD FROM LYSIMETER-GROWN TREES SUBJECTED TO DROUGHT

J. R. BARNETT
Forest Research Institute, New Zealand Forest Service, Rotorua

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ABSTRACT

Rings of collapsed or crushed tracheids, whose thin walls have secondary thickening but lack lignin, have been found in the stems of **Pinus radiata** trees grown in containers and subjected to periodic drought. These rings appear to have arisen as a result of minimal waterings, sufficient to prevent mortality. Ring shake in forest-grown trees may be caused similarly.

INTRODUCTION

The formation of false rings is a well-known effect of drought in conifers (*e.g.*, Glerum, 1970). The cells of these rings, as seen in transverse section, have dimensions similar to those of latewood tracheids, although their walls are not so thick and the tangential walls may have some concavity, particularly near the base of the terminal leader. The presence of such false rings was expected in the stemwood when *Pinus radiata* trees, growing in lysimeters, were subjected to drought. Preliminary microscopic examination showed, however, that what appeared to the unaided eye to be false rings consisted partly of rings of crushed or collapsed tracheids. This note describes the phenomenon in detail, and its possible causes are discussed.

MATERIALS AND METHODS

The wood examined was from trees which were part of an experiment dealing with soil water deficits, described by Jackson *et al.* (1976). Rooted cuttings of *P. radiata* (FRI clones 450, 451 and 460), 27 months old, were planted in evapotranspirometer units of 2.72 m^3 capacity, spaced at 4 × 5 m. After allowing a year for the trees to stabilise, periodic water deficits were applied by excluding rainfall from the surfaces of the units, but not from the tree crowns, at intervals for 5 years. During these periods, soil moisture was maintained at 15% by volume to prevent mortality. Over the 5 years of the experiment, all trees were submitted at various times to year-round deficit, June to November deficit, December to May deficit, or no deficit throughout a year (June to May). During periods of nil deficit, the containers received rainfall, supplemented by watering during natural droughts to keep soil moisture content above 40% by volume.

At the end of the experiment the trees were harvested and stemwood discs were removed for examination. From this material transverse sections were cut for light microscopy, using a sledge microtome. These sections were left unstained, or were stained with safranin and fast green. Samples of the cambium and adjacent xylem and phloem were removed at the same time, and prepared for light microscopy as described elsewhere (Barnett, 1971). The sections thus obtained were examined by bright field, polarisation, and UV fluorescence microscopy.

OBSERVATIONS

Visual examination of discs containing wood formed over the 5-year experimental period revealed that false rings were formed in varying numbers in wood produced during a whole-year drought period. The most prominent rings were found, however, in wood formed during a summer-autumn (December to May) deficit period. Fewer and less pronounced rings were present in wood subjected to winter-spring (June to November) deficit period, while they were virtually absent from wood formed under nil-deficit conditions. This false ring pattern (e.g. Fig. 1) is what would be expected. However, in this example a separation occurred along a ring formed during the autumn of 1971, when the tree was being subjected to a year-round drought. Microscopic examination of the wood of this and similar trees showed that the false rings were more complex than had been thought. Their predominant feature was a ring of

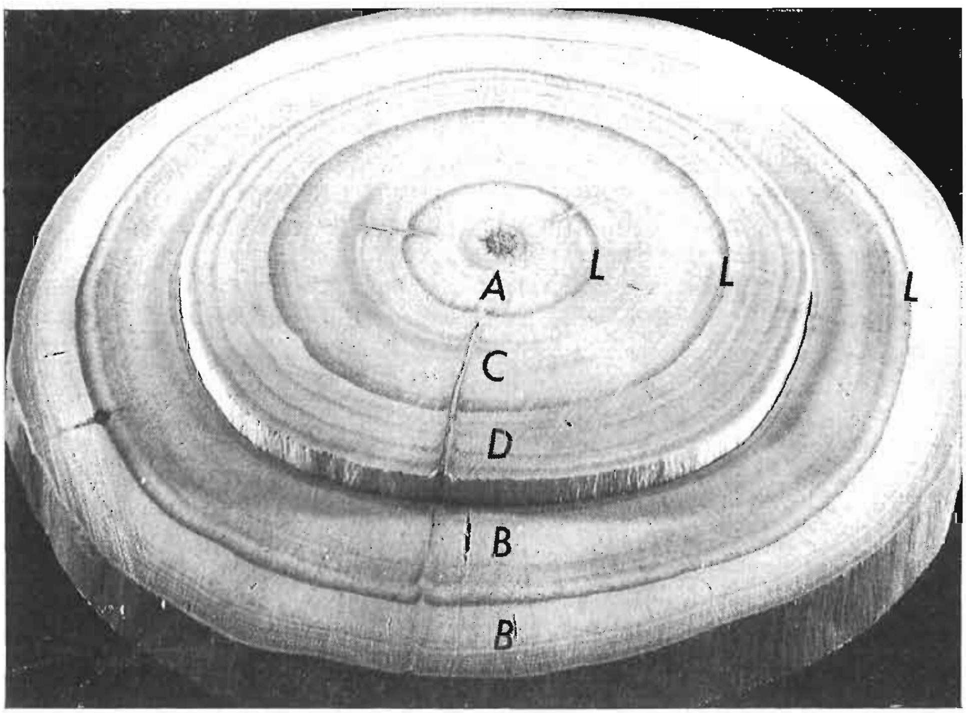

FIG. 1—Stemwood disc of a tree subjected to all four moisture regimes at various times during its 5 years of growth. Latewood bands (L) are clearly visible, as are false rings in drought periods. Note the ring shake.
A — Year during which no drought was applied.
B — Summer-autumn drought.
C — Winter-spring drought.
D — Whole year drought.

highly distorted, compressed or collapsed, thin-walled cells, varying from one to six or more cells radially, sandwiched between uncompressed tracheids. Where the ring of distorted cells was only one or two cells wide, the tracheids on either side were of approximately the same diameter (Fig. 2a). Where the ring of distorted cells was

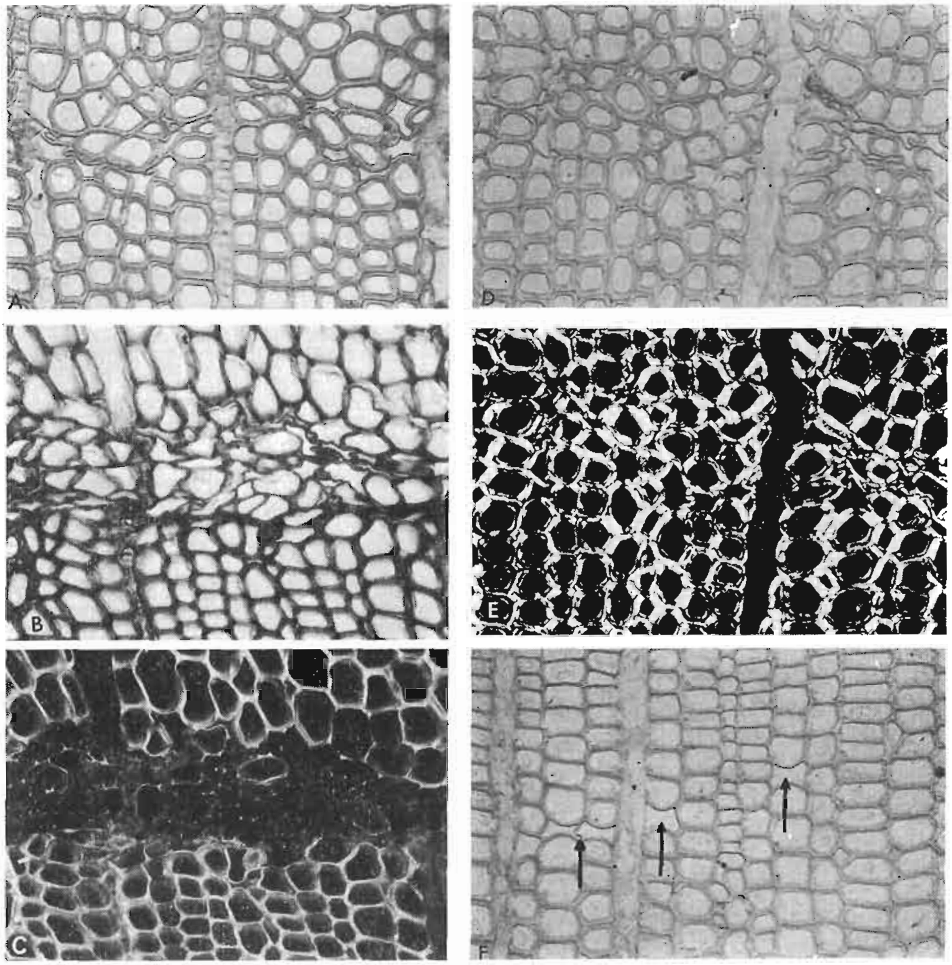

FIG. 2A—TS of fixed and embedded wood showing a ring of crushed cells one or two wide radially, with normal cells on either side.

B—TS of section of untreated wood showing a ring of crushed cells about six wide radially, with false ring cells to the inside and normal earlywood cells to the outside.

C—The area in Fig. 2B viewed using UV fluorescence microscopy. Note the low level of fluorescence in the walls of the crushed cells. Lignin is present in the middle lamellae, and is most pronounced at the cell corners.

D—TS of collapsed ring, bright-field.

E—The above region seen between crossed nicols shows that the walls of crushed cells are birefringent.

F—Isolated thin-walled tracheids (arrows) among normal tracheids.

wider, it was bounded on the outside by normal earlywood cells and on the inside by typical false-ring cells (Fig. 2b). Fluorescence microscopy showed that, while the cells outside the distorted zone were strongly fluorescent and therefore appeared to be fully lignified, cells of the distorted zone fluoresced only weakly in the angles of cell walls as if lignification had been arrested in its earliest stages (Fig. 2c). This observation was confirmed by the use of safranin and fast green stain; normal tracheids and typical false-ring tracheids stained red, while the cells of the distorted zone stained green.

The cell walls of the distorted cells, which were much thinner than those of the normal wood, did nevertheless contain secondary thickening, a fact confirmed by their birefringence between crossed nicols (Figs. 2d and 2e).

Careful examination of undistorted regions of wood formed during drought revealed the presence of isolated thin-walled cells among the normal tracheids. Such cells frequently formed a discontinuous ring within the stem and could represent a milder form of response to drought (Fig. 2f).

Rings of unthickened distorted cells were frequently found near the cambium in trees that were subject to drought just prior to felling, suggesting that the distortion was occurring during or soon after differentiation of the affected tracheids.

DISCUSSION

The rings described above are more complex than the "normal" false rings described by Glerum (1970), and also differ markedly from frost rings as described by Harris (1934) and Glerum and Farrar (1966). They are, however, clearly the result of drought treatments given to the trees during the 5 years of the experiment. From the presence of typical false rings just inside the widest rings of distorted cells, it appears that the greater the drought prior to formation of the larger cells of the distorted ring, the more severe is the ensuing distortion. It is suggested that the rings of distorted cells comprise tracheids formed as a response to the periodic waterings used to maintain soil moisture at 15% volume. In a very dry soil, the water added to restore the 15% volume level concentrates mainly in the surface layers where roots are most abundant and the tree would therefore freely take up water for a time. When this occurred during the period of maximum growth (late summer for this species), the sudden rise in turgor would cause tracheids at the enlarging stage to increase in diameter. But this temporary abundance would soon be depleted, restoring a partial drought and eventually a severe drought once more. The subsequent lowering of turgor in the differentiating tracheids would then either cause collapse, or permit distortion by internal stem forces, which in turn would disrupt and probably terminate differentiation in the affected cells.

A tree growing in a lysimeter in which the drought was not so severe prior to watering, and to which less water had to be added, would produce neither false ring cells nor such a pronounced ring of collapsed cells. In support of this, it was commonly observed that the more severe the drought prior to watering, the more marked was the growth response once the drought was removed (D. S. Jackson, pers. comm.).

Collapse of cells prior to the completion of differentiation would explain both the presence of secondary thickening, and the absence of lignification in cells of the distorted zone, because lignification lags behind cellulose production in the cell walls of tracheids.

The ring shake illustrated in Fig. 1 has resulted from dislocation around a ring of distorted cells, and it seems probable that the same phenomenon could occur in forest trees. For example, a brief period of rain, such as a thunderstorm, occurring in the middle of a severe drought could similarly affect trees growing on shallow soils.

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