Effects of pruning on heartwood formation in Scots pine trees

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ABSTRACT: The object of this study was to investigate the effect of pruning on heartwood formation in mature Scots pine (*Pinus sylvestris* L.) trees. Fifty trees were treated by three different intensive pruning regimes: 42, 60 and 70 percentage of defoliation. After five growing seasons numbers of growth rings were counted and the width and the area of sapwood and heartwood were calculated. The results did not show any proportional increase or decrease in the heartwood area or in the number of growth rings in heartwood associated with the pruning. A statistically significant negative effect of pruning was found on the width of the five most recently formed sapwood growth rings. This decreased growth rate did not influence the ratio of sapwood and heartwood. However, it cannot be excluded that the proportion of heartwood may increase during a longer period. It is concluded that pruning is not a practicable silvicultural method for regulating heartwood formation in mature Scots pine trees.

Keywords: pruning; heartwood; pipe-model theory; Pinus sylvestris L.; sapwood conductivity

The relative amount of sapwood and heartwood in a tree is variable and is related to factors such as species, age, position in the tree, rate of growth and site (HILLIS 1987). The ratio of heartwood to sapwood in Scots pine (Pinus sylvestris L.) trees is an important factor for saw-timber and pulp wood quality. The knowledge how environmental (and other) factors affect the relative amount of heartwood would help choose appropriate trees for different purposes. Since there is a great variation in heartwood content, both between individual trees within stands and between stands, it seems unfeasible to identify heartwoodrich stands or stems using inventory data (cf. BJÖRKLUND 1999). Another possibility may be to develop silvicultural methods that would actively regulate the amount of heartwood. For instance IHARA (1972) suggested that pruning could be used to manipulate trees to form more heartwood for practical use. The influence of pruning, i.e. reduction of the transpiring biomass of the crown, on the amount of sapwood and heartwood was studied and is reported to increase the proportion of heartwood in Chamaecyparis sp. (IHARA 1972), Abies balsamea (MARGOLIS et al. 1988) and in Pinus sylvestris L. (LÅNGSTRÖM, HEL-LOVIST 1991).

According to the "pipe-model theory" (SHINOZAKI et al. 1964) a given unit of conducting tissue (sapwood) is necessary to supply water to a given unit of transpiring foliage. This relationship was established for Scots pine (WHITEHEAD 1978; ALBREKTSON 1984) and for other coniferous species (e.g. KAUFMAN, TROENDLE 1981; WHITEHEAD et al. 1984). The relationship is relatively constant within the homogeneous stand of a species, but it has been found to vary with growing conditions and position in the stem (WHITEHEAD 1978; ALBREKTSON 1984). RUDMAN (1966) and BAMBER (1976) suggested in accordance with this theory that heartwood formation may be a result of adjustment of the sapwood area to a given mass of transpiring foliage. However, other theories were also presented (HILLIS 1987). One of the most accepted theories suggests that heartwood might be formed as a result of the ageing process of ray parenchyma cells (FREY-WYSSLING, BOSSHARD 1959). The age when ray parenchyma cells die varies considerably within species. This age seems to be affected by various factors, such as the relationship between sapwood area and crown size (HILLIS 1987). Thus it is most reasonable to conclude that heartwood formation is probably caused by a combination of both internal and external factors.

If the "pipe-model theory" is true, reductions in needle biomass should result in increased heartwood formation. Previous studies on pruning carried out in young trees support the theory (IHARA 1972; MARGOLIS et al. 1988; LÅNGSTRÖM, HELLQVIST 1991). When evaluating pruning as a possible method to regulate heartwood formation in practical forestry, it is necessary to verify that the effect of pruning also applies to mature trees. Thus the aim of the present study was to examine if reducing the needle

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biomass of mature Scots pine trees would increase the amount of heartwood.

MATERIALS AND METHODS

A homogeneous population of fifty healthy trees of *Pinus sylvestris* L. was selected from a natural stand, situated at Vindeln Experimental Forests (64°14'N,10°46'E, alt. 175), located 67 km north-west of Umeå, belonging to the Swedish University of Agricultural Sciences. The age of the trees, as measured 1.5 m above ground, was ca. 50 year when the experiment started in 1994 and the average height was ca. 17 m. Trees were randomly selected for the different treatments.

The trees were divided into four treatment groups, including 15 control trees (C) that were not pruned. Fifteen trees were moderately pruned (MP) and further 15 trees were heavily pruned (HP). The MP and HP treatments were designed to reduce the needle biomass by 50% and 75%, respectively. The reduction in needle biomass was checked by measuring the dry weight of the needles from the pruned branches at the time of treatment, and the weight of the remaining crown needles of five trees for each pruning treatment felled in September 1994. The results showed that the reductions were approx. 42% and 60% for the MP and HP treatment, respectively. For C, MP and HP trees felled in 1998 (see below for felling schedule), the dry weights of the needle biomasses were also measured.

In another group of five trees the uppermost top part of the tree crown was removed (TC). The reduction in needle biomass for these trees was roughly estimated, by eye, to be ca. 50%. When the trees were felled in 1998, the remaining crown size was found to be, after biomass measurements, 70% compared to the control. All the treatments, applied in June 1994 using a portable sky lift, involved cutting the branches tight by the stem from below for MP- and HP- trees and cutting off the top part of the stem for TC-trees.

The trees within the MP, HP and C treatment sets were then divided into three groups of five, which were felled in September 1994, July 1995 and September 1998 (one group from each treatment on each felling). The five TC trees were harvested in September 1998.

On each sampling collection, 5 cm thick discs were taken from the stem every 0.5 m from the stump up to the first position in the crown where no visible heartwood could be detected. The discs were stored at -2° C until analysis. From the fellings in 1994, 1995 and 1998 discs were analysed (i) from 1.5 m above the stump, (ii) from a position where the stem area was 155 ± 5 cm² and (iii) from a position where the total number of growth rings was approximately 43 ± 2 and 46 ± 2 for TC. The stem area of 155 cm^2 was chosen because it was the area found 1.0 m above the stump in the smallest stem of the sampled trees. Similarly, the number of growth rings, 43, was chosen since this was the lowest number found 1.0 m above the stump. These criteria were applied to compare

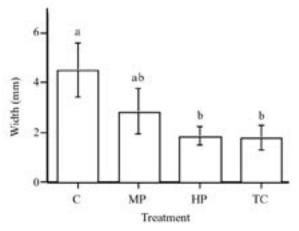


Fig. 1. The average width of the five most recently formed growth rings. Discs were sampled in 1998 and taken from 1.5 m above the stump. C – control, MP – moderately pruned, HP – heavily pruned and TC – top cut. Bars indicate standard deviations (n = 5). Means followed by the same letter are not significantly different ($P \le 0.05$, Tukey's *t*-test)

discs at positions with the same area and with the same physiological age, respectively. For all analysed discs, the numbers of sapwood and heartwood rings were counted and the width of sapwood and heartwood was measured. The sapwood/heartwood border was visualised by staining pinosylvin in the heartwood with sulphanilic acid and nitrite (CUMMINS 1972). Finally, the width of the five most recently grown sapwood rings was measured in the discs taken from 1.5 m above the stump in 1998. The measurements were done in four perpendicular directions for each disc, and mean values were calculated. The sapwood and heartwood areas were estimated as circles, using the width measurements as radii. Stems are not normally perfectly cylindrical, the position of the pith is seldom exactly in the centre, and heartwood extension can be different in different directions. Therefore, these measurements were checked using a planimeter that measured the actual total area and the heartwood area of the discs. This was done for 269 discs taken from different heights of the trees and the linear correlation between the planimeter and the manual measurements was found to be good (data not shown).

RESULTS

Four years after the pruning, the size of the crowns given for the MP and HP treatments was 64% and 49%, respectively, compared to the controls. Thus, the foliage recovered by some 6–9% between 1994 and 1998.

No effect of the treatments on the total number of growth rings was detected even though the discs were standardised by sampling at the same level above ground, at the same stem cross-sectional area or at the same physiological age (Table 1). This was also true of the corresponding total disc areas (Table 1). However, a statistically significant negative effect of pruning was found on the width of the five most recently formed growth rings

Year	Measurement parameters, 1.5 m above the stump	Control (C)	Moderately pruned (MP)	Heavily pruned (HP)	Top cut (TC)
1994	Heartwood, number of growth rings	15.8 (3.3)	17.6 (4.3)	17.6 (4.3)	
	Total number of growth rings	49.8 (5.6)	49.4 (3.5)	50.2 (4.2)	
	Heartwood area	47.2 (21.2)	51.6 (17.4)	61.8 (24.7)	
	Total stem area (cm ²)	195.7 (40.3)	198.1 (39.8)	255.9 (39.0)	
1995	Heartwood, number of growth rings	19.6 (2.4)	17.0 (3.5)	15.2 (3.2)	
	Total number of growth rings	53.2 (3.6)	53.6 (3.8)	50.3 (3.2)	
	Heartwood area	68.2 (22.2)	59.3 (19.3)	41.9 (22.7)	
	Total stem area (cm ²)	214.8 (51.9)	201.8 (27.9)	171.3 (28.8)	
1998	Heartwood, number of growth rings	18.4 (2.9)	18.7 (3.0)	16.5 (2.2)	18.6 (5.2)
	Total number of growth rings	54.8 (2.2)	50.2 (2.8)	52.6 (4.8)	57.0 (2.4)
	Heartwood area	61.2 (21.8)	54.6 (6.4)	52.8 (14.0)	59.17 (21.1)
	Total stem area (cm ²)	219.4 (61.0)	211.1 (29.3)	214.5 (27.9)	226.7 (72.3)
	Measured parameters at equal stem area (155 cm ²)			
1994	Heartwood, number of growth rings	10.6 (1.4)	10.8 (2.8)	8.0 (1.9)	
	Total number of growth rings	41.0 (7.4)	38.8 (9.0)	32.6 (3.8)	
	Heartwood area	26.9 (6.0)	28.6 (8.6)	20.8 (6.0)	
	Total stem area (cm ²)	155.8 (3.1)	152.9 (3.6)	153.3 (2.3)	
1995	Heartwood, number of growth rings	12.8 (4.7)	10.8 (2.4)	11.3 (2.4)	
	Total number of growth rings	41.1 (8.8)	42.2 (3.7)	43.8 (4.9)	
	Heartwood area	37.1 (13.2)	29.1 (13.0)	30.8 (13.2)	
	Total stem area (cm ²)	160.9 (4.9)	154.2 (4.7)	156.2 (3.4)	
1998	Heartwood, number of growth rings	12.2 (4.3)	9.5 (3.4)	11.7 (1.2)	11.3 (2.9)
	Total number of growth rings	42.2 (3.4)	38.0 (5.9)	42.2 (2.0)	42.4 (6.1)
	Heartwood area	31.8 (10.4)	28.0 (11.0)	32.6 (8.1)	31.1 (7.9)
	Total stem area (cm ²)	157.5 (7.2)	155.5 (4.3)	165.4 (4.7)	153.0 (11.8)
	Measured parameters at equal age (43 years)				
1994	Heartwood, number of growth rings	12.81 (2.0)	13.9 (2.6)	13.4 (2.1)	
	Total number of growth rings	43.5 (0.6)	43.0 (0.7)	43.2 (0.4)	
	Heartwood area	36.2 (19.7)	41.0 (15.6)	46.2 (13.3)	
	Total stem area (cm ²)	167.9 (40.4)	181.8 (38.9)	224.7 (34.0)	
1995	Heartwood, number of growth rings	13.2 (1.4)	11.6 (2.4)	11.2 (3.2)	
	Total number of growth rings	42.6 (0.6)	43.6 (0.9)	42.4 (0.6)	
	Heartwood area	48.9 (14.5)	31.6 (10.2)	31.9 (16.3)	
	Total stem area (cm ²)	185.0 (45.4)	155.6 (16.7)	150.6 (16.0)	
1998	Heartwood, number of growth rings	13.2 (3.4)	12.4 (0.7)	12.8 (1.7)	13.1 (3.0)
	Total number of growth rings	44.0 (1.0)	42.2 (0.8)	43.8 (1.3)	46.0 (2.0)
	Heartwood area	36.8 (9.2)	38.2 (2.4)	35.2 (6.2)	37.7 (11.7)
	Total stem area (cm ²)	170.3 (18.5)	182.7 (26.8)	170.4 (10.2)	168.7 (25.6)

Table 1. The amounts of sapwood and heartwood in treated and control trees at three different positions in the trees. Value	es in
parentheses show standard deviations $(n = 5)$	

(Fig. 1). The width of these rings corresponded to 12%, 6%, 6% and 5% of the total stem radius for C, MP, TC and HP, respectively. Assuming that five growth rings were formed during the experimental period, this proves the expected effect of the treatments.

There were no indications that numbers of heartwood rings or heartwood areas increased as a consequence of

the treatments. No such trends were seen in data on discs from the same point above the stump (1.5 m) or with the same area or of the same age (Table 1). The between-tree variation was considerable and no statistically significant differences were found between treatments, either for the relative heartwood area or for the relative number of growth rings in discs from 1.5 m above the stump (Fig. 2).

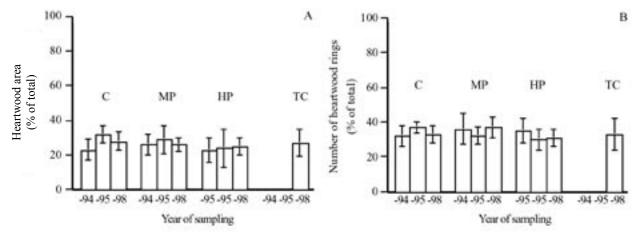


Fig. 2. Relative heartwood area as a percentage of total area (A), and relative number of heartwood growth rings as a percentage of total number of annual rings (B), in discs from 1.5 m above the stump. C – control, MP – moderately pruned, HP – heavily pruned and TC – top cut. Bars indicate standard deviations (n = 5)

This was also true of discs of the same age (Fig. 3) and those of the same area (Fig. 4).

DISCUSSION

The recovery of the crown after pruning was poor since the total crown needle biomass increased by only 6–9%, relative to the control, in the five growing seasons following the treatment. Furthermore, the widths of the annual growth rings produced after the pruning were considerably diminished, compared to the unpruned controls (Fig. 1). Therefore, the pruning probably still affected the trees in 1998, four years after the treatment.

Heartwood formation is suggested to be a process that continues at a constant rate every year, extending centripetally by about one growth ring per year (HILLIS 1987). In the present study, no effects of the different treatments on such a process could be proved since the between-tree variation was great and no minor differences could be verified (Table 1, Figs. 2, 3 and 4).

Pruning did not affect the proportional area of the heartwood or sapwood, contrary to the hypothesis (Table 1, Fig. 2, 3 and 4), and in contrast to previous studies that showed an increased amount of heartwood after pruning (IHARA 1972; MARGOLIS et al. 1988; LÅNGSTRÖM, HEL-LQVIST 1991). However, the earlier studies were done on very young trees and the heartwood border was not defined as in the present study. Both MARGOLIS et al. (1998) and LÅNGSTRÖM and HELLQVIST (1991) studied the amount of water conducting sapwood vs. the nonconducting heartwood and found that pruning resulted in a lower sapwood area than in unpruned trees. LÅNG-STRÖM and HELLQVIST (1991) also found that pruning increased the number of heartwood annual rings in relation to the total number of annual rings. The heartwood border in our study was identified by the presence of pinosylvin, which is specific of heartwood. When comparing heartwood studies it is important to realise that different methods of defining and detecting the heartwood boundary may give conflicting results, which may have caused the discrepancies between our results and those of

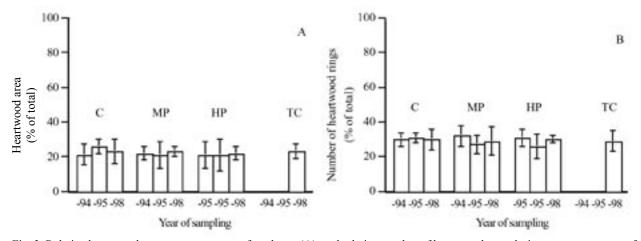


Fig. 3. Relative heartwood area as a percentage of total area (A), and relative number of heartwood growth rings as a percentage of total number of annual rings (B), in discs with approximately 43 growth rings (cf. Table 1). C – control, MP – moderately pruned, HP – heavily pruned and TC – top cut. Bars indicate standard deviations (n = 5)

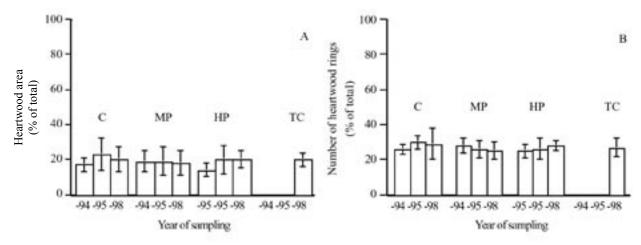


Fig. 4. Relative heartwood area as a percentage of total area (A), and relative number of heartwood growth rings as a proportion of total number of annual rings (B), in discs with an area of ca. 155 cm² (cf. Table 1). C – control, MP – moderately pruned, HP – heavily pruned and TC – top cut. Bars indicate standard deviations (n = 5)

LÅNGSTRÖM and HELLQVIST (1991). The area between the water conducting sapwood and the extractive-rich heartwood, the transition zone, can have a width of 0.4–2.5 cm in Scots pine (RUST 1999). LÅNGSTRÖM and HELLQVIST (1991) stated that their "heartwood" likely represented immobilised sapwood rather than true heartwood *per se*. This suggests that their heartwood may have included the transition zone.

The relationship between foliage area and sapwood cross-sectional area depends not only on the transpiration rate but also on the conductivity of the sapwood (OREN et al. 1986). Pruning by removing branches with a saw juxtaposed to the stem will cause the air to enter the water-transporting xylem and change the conductivity of the sapwood (PRIESTLEY 1932). This may reduce the conductivity of the sapwood and thereby alter the relationship between the water-conducting sapwood and the mass of the foliage. Thus, pruning should affect the sapwood area according to the "pipe-model theory", but in our study this putative effect was not reflected in increased heartwood content. However, if the air enters and accumulates in the transition zone, it may initiate heartwood formation (HARRIS 1954; OHASHI et al. 1991).

Another explanation for the absence of a pruning effect on heartwood formation is that the reduction of the crown may have been too extensive, causing carbohydrate deficiency. KIMBALL et al. (1998) previously showed that pruning resulted in reduced growth and decreased carbohydrate content of the vascular tissue. The reduced growth rate (Fig. 1) is also an indication for carbohydrate deficiency since carbohydrate concentration is closely tied to growth in the cambial zone (KOZLOWSKI, PALLARDY 1997). This could then have led to a deficiency of substrates involved in the formation of heartwood extractives such as pinosylvin (HILLIS et al. 1962; LORIO, SOMMERS 1986; FISCHER, HÖLL 1992). However, KIMBALL et al. (1998) showed no effect of pruning on the terpene concentration of the vascular tissue. Whether the transition zone increased (without formation of pinosylvin) could not be detected since the heartwood border was identified by the distribution limits of pinosylvin. When the needle biomass recovers and the carbohydrate availability for synthesis of extractives increases, complete heartwood formation may occur. Therefore it is possible that the effects of pruning on heartwood formation would only have been seen if the study had continued over a longer period. Reductions in the current annual growth over a prolonged period would also cause relative increases in heartwood, as a consequence of the decreased width of the sapwood.

In conclusion, this study was carried out to see whether pruning increased the amount of heartwood in mature trees. The results show that the amount of heartwood is not affected by pruning over a period of five growing seasons, although it cannot be excluded that the proportion of heartwood may increase over a longer period. Thus the results so far collated indicate that pruning is not a practicable silvicultural method for regulating heartwood formation in Scots pine.

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Vliv vyvětvování na tvorbu jádrového dřeva u borovice lesní

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ABSTRAKT: Cílem práce bylo zkoumat účinek vyvětvování na tvorbu jádrového dřeva dospělých stromů borovice lesní (*Pinus sylvestris* L.). Analýza byla provedena na padesáti stromech po aplikaci tří režimů vyvětvování; tyto tři režimy vyvětvování představovaly defoliaci 42 %, 60 % a 70 %. Po pěti vegetačních obdobích byl zjišťován počet letokruhů a vypočítána šířka a plocha bělového a jádrového dřeva. Výsledky neukázaly proporcionální zvětšení ani zmenšení plochy jádrového dřeva nebo počtu letokruhů ve vazbě na sílu vyvětvování. Negativní statisticky průkazný účinek vyvětvování byl nalezen pro šířku letokruhů vytvořených v bělové části dřeva v posledních pěti letech po zásahu. Snížená rychlost tloušťkového růstu však poměr mezi bělovým a jádrovým dřevem neovlivnila. Přesto nelze vyloučit, že se podíl jádrového dřeva může během delšího časového období zvýšit. Závěrem je nutné konstatovat, že vyvětvování není pěstební opatření použitelné k regulaci tvorby jádrového dřeva u dospělých jedinců borovice lesní.

Klíčová slova: vyvětvování; jádrové dřevo; cévní model; Pinus sylvestris L.; vodivost běli

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