THE ANNUAL RHYTHM OF ACTIVITY OF THE LATERAL MERISTEMS (CAMBIUM AND PHELLOGEN) IN PINUS HALEPENSIS MILL. AND PINUS PINEA L.

by

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Summary

The annual rhythms of cambial and phellogen activity in *Pinus halepensis* and *P. pinea* were investigated. Under natural conditions the cambium of *P. halepensis* begins its activity in autumn, enters a quiescent period during midwinter, resumes activity towards spring and enters a second rest period in summer. The ring border is formed during summer. Irrigated plants growing outdoors were active almost all the year round.

The cambium of *P. pinea* is active between April and November and enters a true winter dormancy.

The duration of xylem production exceeded that of the phloem. More xylem than phloem cells were formed. The phellogen was active during a short period only.

Pinus halepensis seems to follow the Mediterranean climate patterns whereas *P. pinea* follows the pattern of a colder climate.

Key words: Periodicity, phellogen, phloem, *Pinus*, vascular cambium, xylem production.

Introduction

Pinus halepensis and *P. pinea* are common in the East and North Mediterranean countries, both naturally and in cultivation (Davis, 1965; Feinbrun, 1959; Mirov, 1967; Polunin & Huxley, 1967; Zohary, 1966, 1973). In spite of their economic value, only few investigations have been made concerning the effect of various environmental factors on the growth rhythm and wood production of these species. The annual rhythm of the cambium and phellogen activity in *Pinus halepensis* and *P. pinea* were therefore followed, using the radiological method (cf. Waisel & Fahn, 1965).

Materials and Methods

Plant material

Pinus halepensis Mill. – Young saplings (2 years old) and 12-year old *P. halepensis* trees were used for this investigation. The young plants were grown outdoors, as well as under controlled conditions in growth chambers, at Tel Aviv University. The trees were examined in the Forest Research Station at Ilanoth, where they grow without irrigation. Four-year old plants, grown without irrigation at Ilanoth were also examined. Wood samples for analysis were taken from the shoot, transition region and root of the 2- and 4-year old plants and from the branches of the 12-year old trees.

Pinus pinea L. – Young saplings, one and a half years old, of *P. pinea* were used for this investigation. The plants were grown outdoors in Tel Aviv. Similar plants were grown under controlled conditions in growth chambers. Wood samples for analysis were taken from the shoots, transition region and roots of the plants. Seedlings of *P. pinea* were germinated and grown under controlled daylength and temperatures for eight months. Samples for wood analysis were taken from the root and the shoot of these seedlings.

Environmental conditions

The effect of water stress, daylength and temperature were examined with young plants only. High and low water stresses were given by different irrigation regimes. The daylength treatments were 8 hours for a short day and 16 hours for a long day. Light intensity was in both chambers 4.1 Wcm^{-2} obtained from VHO lamps. Two temperature treatments were given: high temperature treatment (25°C ± 1°C) day and night, and low temperature treatment (12° C at night and 18°C by day).

Methods of examination

Histological and radiological methods of examination were used. Plants were labelled with $^{14}CO_2$, sectioned and micro-autoradiographed (Waisel & Fahn, 1965). Whenever needed, sections were stained either with Reactif Genvois or with Safranin-Fast Green (Johansen, 1940; Jensen, 1962).

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Experiments and Results

Pinus halepensis

The annual rhythm of activity in young plants growing outdoors. The annual rhythm of cambial and phellogen activity was followed in young plants growing in a sandy-loam soil in Tel Aviv during the years 1978–80. The plants were irrigated. A group of six plants was labelled with $^{14}CO_2$ once a month during one year. Samples of the labelled shoot, transition region and roots of each specimen were taken for examination one month after the radiological treatment. Groups of six plants each were labelled twice, at six months intervals and were sampled a month after the second labelling.

The results are summarised in Table 1, Fig. 1 and Plate 1.

The cambium of these irrigated young plants was active throughout the year with low rates of activity during the period November–December. During this year no ring border could be observed.

Phloem production in the investigated plants was observed twice a year; during the spring (March–April) and the autumn (end of August, September and October).

Table 1. Annual rhythm of cambial and phellogen activity in 2-year old plants of *Pinus halepensis* grown outdoors under irrigation.

Group of plants labelled once

Labelling date	*Sampling date*	*Xylem*	*Phloem*	*Phellogen*
10. 4.78	7. 5.78	+++	++/+++	++/+++ in patches
7. 5.78	7. 6.78	++	–	–
7. 6.78	10. 7.78	++	–	–
10. 7.78	14. 8.78	++	–	–
14. 8.78	11. 9.78	++	–/+	+
11. 9.78	8.10.78	++/+++	+/++	–
8.10.78	8.11.78	+++	++/+++	–
8.11.78	6.12.78	+/–	–	–
6.12.78	15. 1.79	–/+	–	–
15. 1.79	15. 2.79	++/+++	–	–
15. 2.79	14. 2.79	++	–	–
14. 3.79	9. 4.79	+++	+/++	++ lenticels only

Group of plants labelled twice

Labelling dates	*Sampling date*	Xylem	
		First labelling	*Second labelling*
10. 4.78 & 8.11.78	6.12.78	+++	+/– no ring border between labelled rings
10. 4.78 & 1.12.78	15. 1.79	+++	–/+ ibid.
7. 5.78 & 15. 1.79	15. 2.79	+++	+++ ibid.
7. 6.78 & 15. 2.79	14. 3.79	++/+++	++ ibid.
10. 7.78 & 14. 3.79	9. 4.79	+++	+++ ibid.

Group of plants labelled once or twice and sampled after two years

10. 4.78	16. 4.80	No ring between labelled rings
7. 5.78 & 15. 1.79	16. 4.80	ibid.

+++ = highly active; ++ = active; + = slowly active; – = inactive; +/– = active in patches.

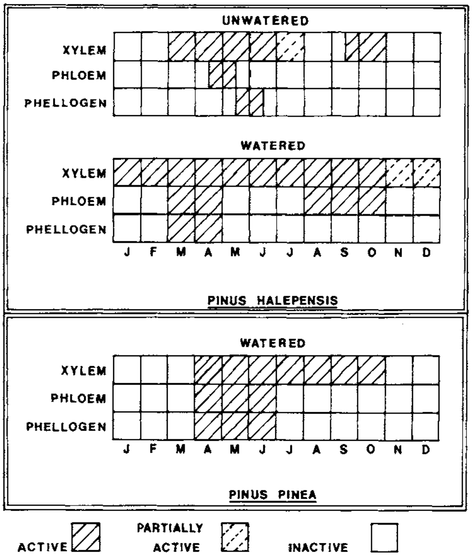

Fig. 1. The annual rhythm of cambial and phellogen activity.

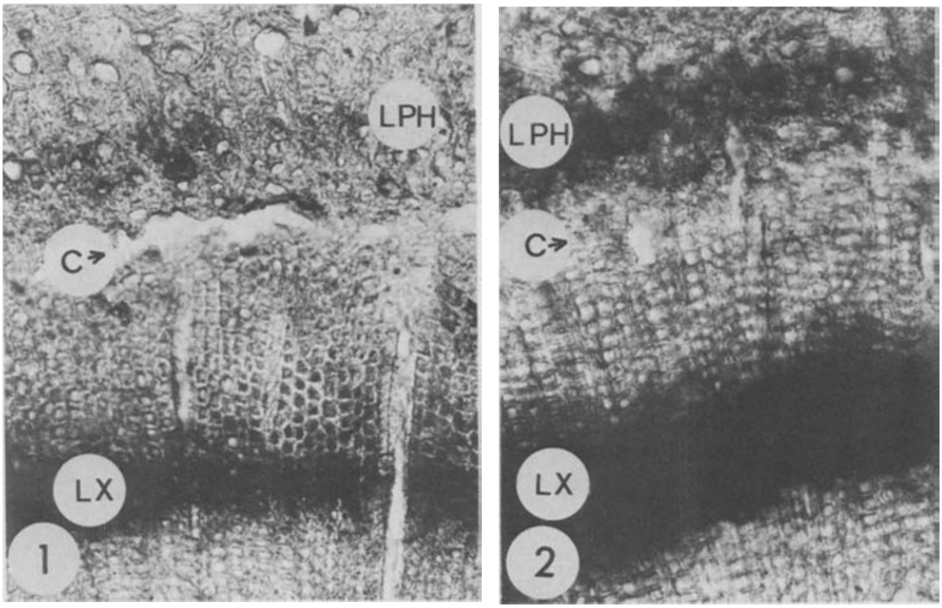

Plate 1. Microautoradiographs of cross-sections of the shoot (1), and root (2) of a 2-year old *Pinus halepensis* plant growing outdoors under irrigation in Tel Aviv (x 135). $^{14}CO_2$ labelling was given on 11 September 1978. Samples were taken on 10 October. – LX = xylem label; LPH = phloem label; C = cambial zone.

The primary phellogen in the very same plants was active mainly during March and April; low activity was distinguished also during August.

Ring formation in 4-year old plants. Two 4-year old plants of *Pinus halepensis* growing in Ilanoth, without irrigation, were labelled once with $^{14}CO_2$. Samples were taken from the shoot, transition region and root one year after labelling. Results are given in Plate 2. As can be seen in those two young specimens, a ring border was produced both in the shoot and root, while a second ring which seems to be a false ring was formed later only in the shoot (Plate 2: 1 & 2).

The annual rhythm of activity in 12-year old trees. Six 12-year old *Pinus halepensis* trees growing in Ilanoth were investigated during the years 1978–79. Each month six branches were labelled, one branch on each tree. The branches were sampled one month after labelling. Results are summarised in Table 2, Fig. 1 and Plate 2.

As can be seen, two periods of xylem production took place in those branches during the year. The first period took place between the end of March and June, and the second during the end of August to November. Phloem was produced only during May and phellogen was found to be active during June only.

Effects of daylength and temperature on cambial activity in joung plants. In another set of experiments 2-year old *Pinus halepensis* plants were exposed to various combinations of daylength and temperature in growth chambers. Experiments were conducted between June and November, 1978, and between January and April, 1979. Forty plants were labelled with $^{14}CO_2$ and transferred to the growth chambers for one, two, three or five months. Samples of ten plants were taken for each period from the shoot, transition region and root. Results are summarised in Table 3.

As can be seen from this table, more xylem cells were formed under LD conditions than under SD conditions in plants exposed to low and probably also to high temperatures. Plants which were transferred, during the summer months, from outdoor conditions to low temperatures, showed a change in the type of xylem cells from latewood to earlywood (Plate 3).

Pinus pinea L.

The annual rhythm of activity under outdoor conditions. The annual rhythm of cambial and phellogen activity was followed in young plants growing outdoors in Tel Aviv during the years 1980–81. The plants were irrigated. Six plants were labelled with $^{14}CO_2$ each month. Another group of six plants was labelled once and then left for a year before sampling. Results are summarised in Table 4, Fig. 1 and Plate 4.

The data show that the cambium of these plants was active from the middle of March to the middle of September. Xylem was produced during the whole period, while phloem was

Table 2. Annual rhythm of cambium and phellogen activity in 12-year old trees of *Pinus halepensis* growing outdoors in Ilanoth.
Numbers are the number of xylem layers produced between labelling and sampling.

Labelling date	*Sampling date*	*Number of xylem layers*	*Type of wood*	*Phloem*	*Phellogen*
30. 4.78	31. 5.78	6–8	transition from earlywood to latewood	+	–
31. 5.78	26. 6.78	4–5	latewood	–	+
26. 6.78	24. 7.78	–	–	–	–
24. 7.78	27 8.78	–	–	–	–
27. 8.78	27. 9.78	1–2	earlywood near the cambium	–	–
27. 9.78	24.10.78	1–2	earlywood near the cambium	–	–
24.10.78	23.11.78	2–4	earlywood near the cambium	–	–
23.11.78	25.12.78	–	–	–	–
25.12.78	24. 1.79	–	–	–	–
24. 1.79	1. 3.79	–	–	–	–
1. 3.79	28. 3.79	–	–	–	–
29. 3.79	26. 4.79	4–5	earlywood	–	–

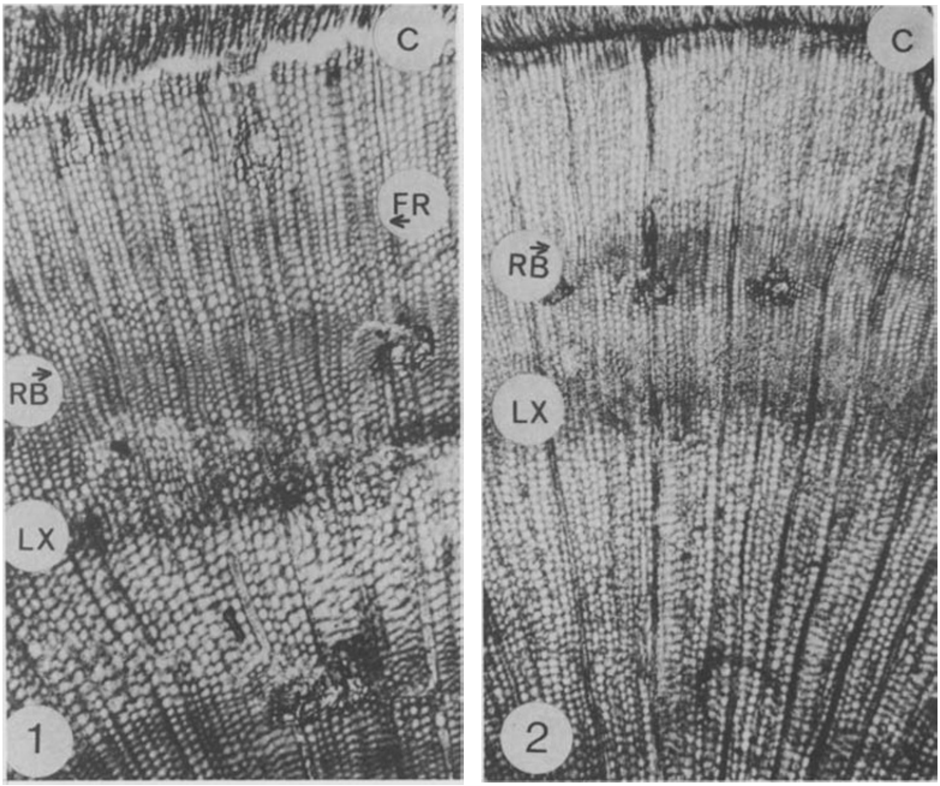

Plate 2. Microautoradiographs of cross-sections of the shoot (1) and root (2) of a young 4-year old *Pinus halepensis* plant growing naturally outdoors in Ilanoth (x 135). – 1 & 2: Labelling was given on 30 April 1978. Samples were taken on 26 April 1979. – LX = xylem label; RB = ring border; FR = false ring; C = cambial zone.

produced during the spring months April–May only. The phellogen was also active during the spring period only.

The effect of water stress on cambial activity. The effects of water stress on cambial activity were investigated in another group of plants. Experiments were conducted during mid-April to mid-June, 1980. Prior to the onset of the experiments the plants were treated with $^{14}CO_2$. Irrigation was withheld two weeks after labelling. When signs of water stress became visible, approximately two weeks after the drought period had begun, watering was resumed for another period of one month. Samples for analysis were then taken from three sites along the shoot, from the transition region and from the root.

In some of the plants water stress had no apparent effect on the type of wood. In others, 2–3 layers of small-diameter tracheids with thick walls were produced consequently (Plate 5).

Effects of daylength and temperature on cambial activity. In another set of experiments, 2-year old plants were exposed to various combinations of daylength and temperature. Experiments were conducted during the period of activity, i.e. between April and August. Plants were labelled with $^{14}CO_2$ on April 25th, 1980 and transferred to the growth chambers. Three sets of ten plants were used. One set was sampled on July 17th, 1980; a second set was sampled on September 17th, 1980, and another set of ten plants was transferred from one combination of daylength and temperature to the

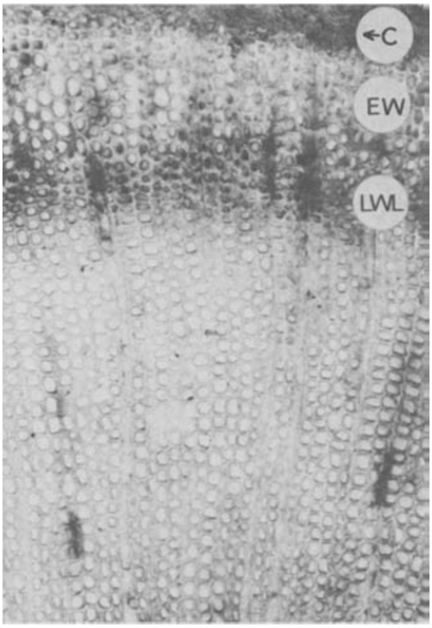

Plate 3. Microautoradiograph of a cross-section of the shoot of a 2-year old *Pinus halepensis* plant growing under irrigation. The plant was transferred on 13 June 1978 from LDHT conditions (outdoors) to LDLT conditions (16 hours daylength); 12°C night temperature, 18° C day temperature. The sample was taken on 19 July 1978. $^{14}CO_2$ labelling was given on 6 June 1978 (x 135). – LWL = latewood labelled, EW = earlywood produced (under LDLT conditions).

other one on July 17th, 1980 and sampled on September 17th, 1980. Results are summarised in Table 5.

As can be seen from this table, the maximal number of cells was produced outdoors. Under LD conditions more cells tended to be produced. No difference in the type, or in the size of the tracheids was observed under the different combinations of daylength and temperature.

The effects of daylength and temperature on xylem and phellogen activity in young plants germinated and grown under controlled conditions. Pinus pinea seedlings which were germinated and grown for eight months under LDHT and SDHT conditions, as well as outdoors (October 1980–June 1981), were examined. The xylem formed under LD treatment was of the earlywood type, whereas under SD conditions latewood was formed (Plate 6).

Discussion

Histological studies of the annual rhythm of cambial activity in *Pinus halepensis* in Israel yielded discrepant results. According to Gindel (1944, 1947), *P. halepensis* did not grow during the larger part of the winter because of the prevailing low temperatures. The cambium of trees in the Judean Mountains was active during the period February–August only, and stopped its activity then because of water shortage. On pine sites of low elevation, e.g. Mount Carmel, the cambium was active also during September–October, i.e., during the early rainy season, which is accompanied by favourable temperatures. The trees entered a period of inactivity later in the season when temperatures dropped (Gindel, 1944). On the other hand, Oppenheimer (1945) found that the cambium of suppressed aleppo pine trees grown without irrigation near Jerusalem, was active from April to September. In semi-dormant trees the cambium was active from March to November and in a vigorous specimen the cambium remained active throughout the year.

Radiological examination of branches of non-irrigated adult *P. halepensis* trees revealed that the cambium was active twice a year, i.e., during October–November and during April–June. Activity of the cambium began in the autumn when temperatures dropped and water became less limiting. Cambium ceased its activity following a drop in temperatures. On the other hand, in young plants grown outdoors under irrigation, the cambium remained active throughout the year. It seems therefore, that rest rather than dormancy characterises the cessation of cambial activity in *P. halepensis* during the winter.

The formation of the annual ring border in *P. halepensis* depends on the specific ecological conditions of the habitat: in Israel it is formed in summer, while in Italy and Southern France it is formed in autumn (cf. Messeri, 1948; Serre, 1976). Phenological investigations in Greece, of adult unwatered *P. halepensis* trees showed that the main extension growth occurred during February–June (Diamantoglou & Kull, 1982).

Comparison of cambial activity in the roots and shoots of irrigated young plants of *P. halepensis* and *P. pinea* showed no difference in the type of the cells and the duration of cambial activity between root and shoot. Various envi-

Table 3. Effect of daylength and temperature on wood production in *Pinus halepensis* plants. Numbers are number of xylem cells produced in a radial file between labelling and sampling.

I. Plants labelled during summer (7. 6. 78)
Duration of experiments: a) 28 days (13. 6. 78 – 10. 7. 78)
b) 101 days (13. 6. 78 – 22. 9. 78)
c) 143 days (13. 6. 78 – 2. 11. 78)

	Outdoors (summer) (= LDHT)	LDLT			SDLT		
	28 days	28 days	101 days	143 days	28 days	101 days	143 days
Shoot	4–5	7–8	12–13	18–20	5–6	7–8	8–9
Transition region	4–5	7–8	12–13	18–20	4–5	7–8	8–9
Root	4–5	5–6	12–13	15–17	4–5	7–8	7–8

II. Plants labelled during winter (15. 1. 79)
Duration of experiment: 70 days (21. 1. 79 – 2. 4. 79)

	Outdoors (winter) (SDLT–LDLT)	LDHT	SDHT
Shoot	7–8	3–4	2–3
Transition region	7–8	3–4	2–3
Root	7–8	3–4	2–3

LDHT = long day, high temperature; LDLT = long day, low temperature; SDLT = short day, low temperature; SDHT = short day, high temperature.

ronmental conditions, i.e., photoperiod and temperature affected the root and the shoot in the same way. This is not new, as similar results were obtained for *P. sylvestris* and *Picea sitchensis* (Denne, 1972).

On the other hand, in naturally growing young plants of *Pinus halepensis*, false ring formation was obvious in the shoot only. This false ring was probably the outcome of changes in temperature during the growth season, which is much more severe in the environment of the shoot than of the root. A similar phenomenon could be distinguished also in *Cupressus sempervirens*, i.e., only one ring border was formed during the year in the main root while two ring borders were obvious at the same period in the stem (Liphschitz et al., 1981).

Cambial activity involves production of cells on both sides of the meristem. Phloem production has been reported to begin before, after or simultaneously with xylem formation and to cease later or simultaneously with it (Bannan, 1955; Waisel et al., 1966; Philipson et al., 1971).

The number of xylem cells in *Pinus halepensis* and *P. pinea* produced at any period examined, and the duration of their formation exceeded that of the phloem cells. All the annual production of phloem cells in unirrigated *P. halepensis* trees was concentrated in one month only. In irrigated plants, phloem elements were produced during three months in *P. pinea* and during two periods of a total of five months in *P. halepensis*. The ratio xylem : phloem cells for these months of phloem production for both species was approximately 3 : 1. The average ratio of xylem to phloem cells for the whole season of xylem production was 6 : 1. Similar ratios of xylem to phloem were observed for irrigated *Cupressus sempervirens*, both for the whole season and for the season of phloem production only (Liphschitz et al., 1981).

Another point of interest is the interrelationships between the cambium and the phellogen. The rate of phellogen activity in *P. halepensis* is very low as compared with that of the cambium. Under natural conditions phellogen activity

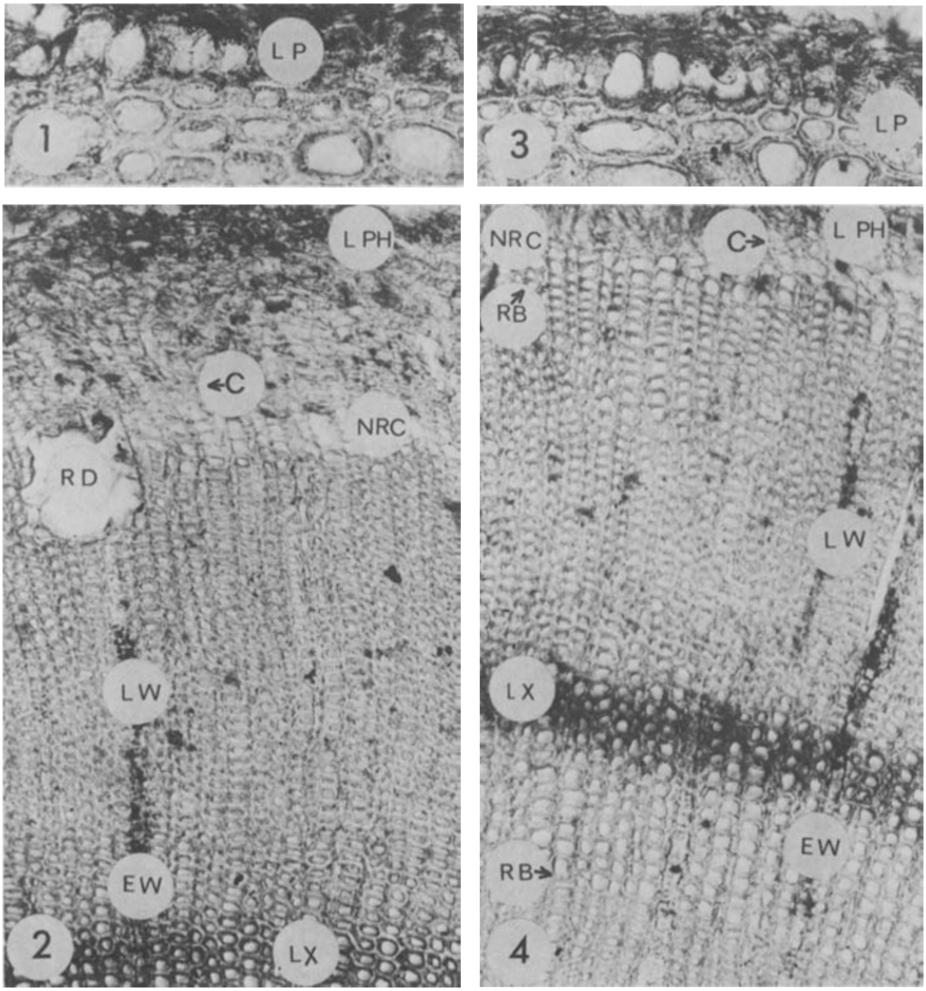

Plate 4. Microautoradiographs of cross-sections of the shoot (1 & 2) and the root (3 & 4) of a 2-year old *Pinus pinea* growing outdoors under irrigation in Tel Aviv (x 120). $^{14}CO_2$ labelling was given on 22 April 1979. Samples were taken on 20 April 1980. – LX = labelled xylem; LPH = labelled phloem; LP = labelled phellogen; RD = resin duct; EW = earlywood; LW = latewood; RB = ring; NRC = new ring cells.

yielded only a few layers of cells during one month only. Irrigation prolonged the duration of activity of both meristems. Similar results were also obtained for irrigated plants of *Pinus pinea*. In this species the rate of phellogen activity was also very low as compared with that of the cambium.

The duration of activity of both meristems differed. In both pines the cambium continued to be active even when phellogen ceased its activity. Similar independent rhythm of activity of the two meristems was previously reported for *Robinia pseudacacia* (Liphschitz et al., 1965; Waisel et al., 1967), *Acacia raddiana* (Arzee et al., 1970) and *Cupressus sempervirens* (Liphschitz et al., 1981).

In well adapted woody plants the annual rhythm of cambial activity should be similar to that of the climatic rhythm. The correlation is a conservative characteristic of the plant and may, therefore, serve as one of the best indicators to their origin (Fahn, 1953). Adaptation of plants to the East Mediterranean climatic rhythm should be characterised by one active growth season, i.e., during the mild and wet autumn, winter and spring, or by two periods of inactivity during the cold winter and the dry and warm summer months, when winter is extremely cold (cf. Mitrakos, 1980). Indeed, the cambial rhythm of *Pinus halepensis* shows such a type of activity and is thus well adapted to the climate of the East Mediterranean region. On the other hand, the cambium of *P. halepensis* trees in Southern Europe was active throughout the summer and exhibited only one period of inactivity (cf. Messeri, 1948; Serre, 1976). It is tempting to assume that adaptation in this species is not completed because of the lack of summer dormancy and the existence of a rest period.

Table 4. The annual rhythm of cambial and phellogen activity in 1–2-year old irrigated *Pinus pinea* plants, grown outdoors in Tel Aviv.

Labelling date	*Sampling date*	*Xylem*	*Phloem*	*Phellogen*
22. 4.80	20. 5.80	+	+	+
20. 5.80	17. 6.80	+++	++	+
17. 6.80	17. 7.80	++	++/+	+
17. 7.80	17. 8.80	++	–	–
17. 8.80	16. 9.80	++	–	–
16. 9.80	16.10.80	+	–	–
16.10.80	16.11.80	–	–	–
16.11.80	15.12.80	–	–	–
15.12.80	14. 1.81	–	–	–
14. 1.81	19. 2.81	–	–	–
19. 2.81	18. 3.81	–	–	–
18. 3.81	17. 4.81	–	–	–

+++: highly active; ++: active; +: slowly active; –: dormant.

Number of cells produced by the cambium:

Period	*Number of xylem cells produced*	*Number of phloem cells produced*	*Xylem/phloem ratio*
April–June	21	6	3 : 1
April–September	36	6	6 : 1

Table 5. Effects of various combinations of daylengths and temperatures on xylem production in *Pinus pinea* plants.
Numbers represent xylem cell layers produced.

Labelling date	*Sampling date*	*Outdoors*	LDHT	SDHT	LDLT	SDLT
25. 4. 80	17. 7. 80	21	13	4	–	–
25. 4. 80	17. 9. 80	31	20	7	–	–
17. 7. 80	17. 9. 80	10	7	3	5	3

LDHT = long day, high temperature; LDLT = long day, low temperature; SDLT = short day, low temperature; SDHT = short day, high temperature.

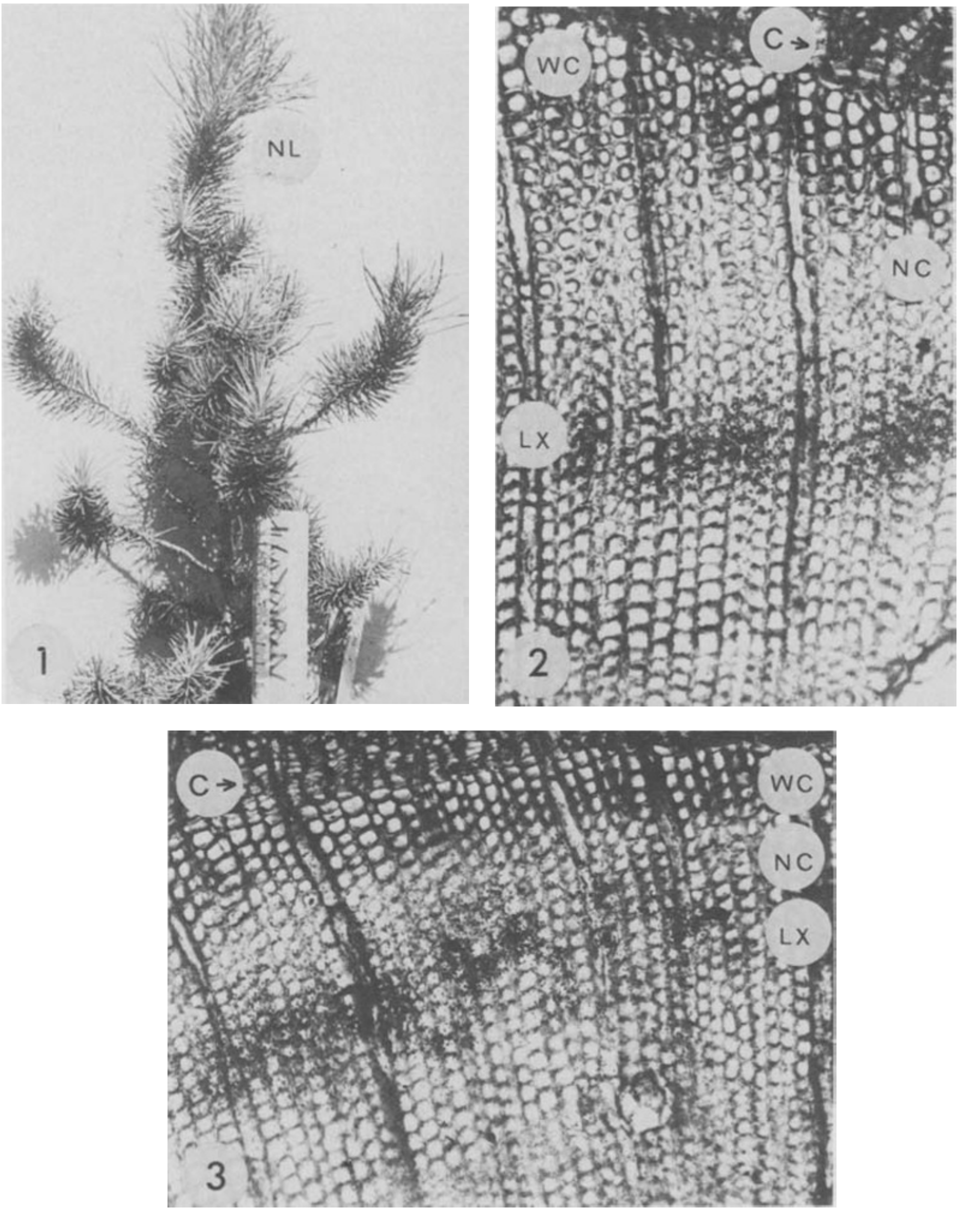

Plate 5. General view (1) and microautoradiographs of cross-sections of the stem (2) and root (3) of a 2-year old *Pinus pinea* growing outdoors in Tel Aviv (2 & 3 x 120). $^{14}CO_2$ labelling was given on 22 April 1978; irrigation was withheld on 6 May 1978; irrigation was resumed on 19 May 1978. Samples were taken on 17 June 1978. – NL = new leaves; LX = labelled xylem; NC = narrow cells; WC = wide cells; C = cambial zone.

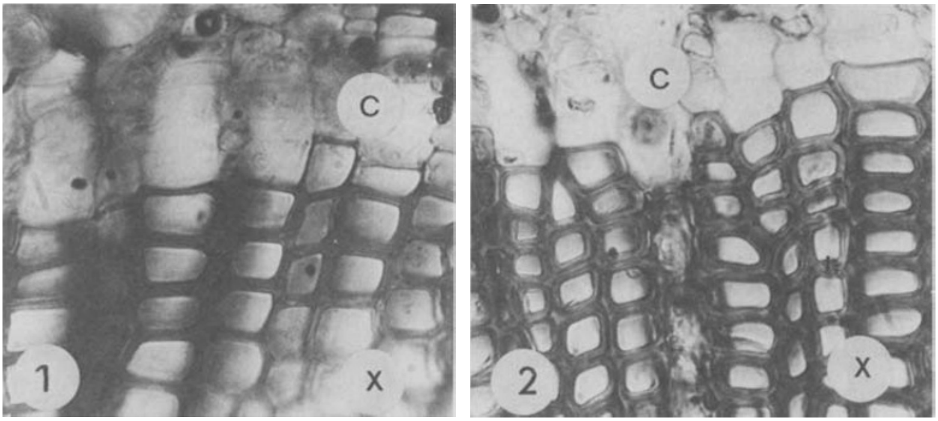

Plate 6. Cross-sections of shoot of a 6-months old *Pinus pinea* growing under irrigation. Plants were germinated and grown under LDHT (1) and SDHT (2) conditions (x 500). – X = xylem; C = cambial zone.

Pinus pinea which was shown to be sensitive to low winter temperatures and summer dryness in France (Cabanettes & Rapp, 1981) maintains in Israel the rhythm of activity of the temperate region where winter is unfavourable for tree growth. Winter dormancy is known in our region also in other genera of the Pinaceae, i.e. in *Cedrus libani* (Fahn et. al., 1979) and *Pinus brutia* (Heth, 1968). The pattern of activity of *Pinus pinea* suggests that this species has presumably originated in high elevations of the Mediterranean region or in the temperate region.

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