

STUDIES ON THE FORMATION OF EPICORMIC SHOOTS ON EUCALYPT STEM SEGMENTS*

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Epicormic shoots occur on many forest trees including eucalypts. They are formed from bud-producing tissue situated in the bark at the ends of the epicormic bud strand. The strands originate in leaf axils, and grow radially outward at almost exactly the same rate as diameter growth of the stem (Jacobs 1955). The epicormic bud is normally dormant but may develop into a shoot within the live crown, aiding in crown maintenance, or on the clear bole where it may seriously reduce timber quality as a knot, gum vein, or a site for fungal infection.

In undisturbed forest stands, epicormic shoots on the boles occur most frequently on the least vigorous trees but damage to the crown, thinning, and pruning may all stimulate shoot production even on dominant trees (Cosens 1952; Bernsten 1961; Webb and Grose 1962). Epicormic shoots are more abundant on the warmer or more exposed sides of trees (Wahlenberg 1950; Ward 1966), and on the upper bole (Jemison and Schumacher 1948; Bruner 1964; Ward 1966).

The most generally accepted theory of epicormic shoot formation is that it is controlled by a hormone inhibitor (assumed to be an auxin) produced in the crown. Recently, Bowersox and Ward (1968) showed that auxins at concentrations from 0.25 to 1.0% inhibited epicormic shoot formation on white oak segments. However, some observations of epicormic shoot formation, such as their occurrence on the upper compared with the lower bole, and their association with existing shoots (Ward 1966), are difficult to reconcile with the auxin theory. Furthermore, the factors triggering epicormic shoot formation on forest trees following management practices such as thinning are not defined.

Field studies on the physiology of epicormic shoot formation are difficult to interpret because of the interrelationships between many potential factors such as light, temperature, and the availability of water and nutrients.

In this paper, the effects of environmental and hormonal factors on epicormic shoot formation on isolated stem segments are described.

Materials and Methods

Since epicormic shoots form from dormant bud strands, and not directly from the accessory bud-producing tissue in the leaf axil, leafless segments of 2-year-old branch wood possessing dormant buds were used. A tree was felled and all live branches were brought to the laboratory. Straight leafless segments (c. 10 cm long) were selected and surface-sterilized by shaking in calcium hypochlorite (5% w/v) for 1.5 hr. The segments were then rinsed in sterile water, fresh surfaces were exposed at each end, and the segments were inserted singly into 15 ml of 1.5% agar medium in 25 by 150 mm boiling tubes stoppered with cotton plugs. Five or ten segments were used in each treatment and one tree provided sufficient segments for any one experiment, thus eliminating complications due to genotypic variation.

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All media and implements were sterilized by autoclaving at 15 lb/in² for 20 min, and all manipulations were carried out under sterile conditions.

Segments from trees of *Eucalyptus polyanthemos* Schauer, 50 or more years old, were used since this species produces epicormic shoots under natural conditions, and was readily available.

Results and Discussion

Epicormic shoots formed from the dormant bud tissue in the experimental system (Fig. 1), and, although no treatment was successful in producing at least one shoot from every segment, the following results were obtained:

- (1) Sucrose (4% w/v), in the presence and absence of mineral nutrients, vitamins, and amino acids, inhibited shoot formation.
- (2) A temperature regime of 21/17°C day/night temperature reduced and slowed shoot formation compared with 25°C constant temperature, and 27/22, 30/20, and 30/25°C day/night temperatures.
- (3) High light intensity was not a critical requirement, some segments producing shoots at intensities as low as 200 f.c.
- (4) Growth substances [gibberellic acid (GA₃), 1–100 p.p.m.; indoleacetic acid (IAA), 1 and 10 p.p.m.; and kinetin, 5 p.p.m.], whether incorporated in the agar medium or taken up in solution by the segment before severance from the branchlet, inhibited shoot formation.
- (5) Water alone completely inhibited shoot formation, best production occurring at an agar concentration of 1% or greater.
- (6) Preliminary experiments using commercial cellophanes as filters of sunlight indicated that red light may stimulate shoot production, and green, blue, yellow, and orange lights inhibit it.

Variability between experiments in shoot production from control segments (in 1.5% agar alone) complicated the results but, when all results from these segments were plotted against time of collection, a definite seasonal pattern emerged (Fig. 2). Shoot production was greatest in winter and least in summer, independent of the conditions under which the segments were placed, indicating some form of endogenous control. Sucrose at concentrations of 0.5–1.5% failed to stimulate shoot production on segments collected in summer.

The winter maximum occurs at a time when cambial activity of the parent tree may be expected to be at a minimum (Amos, Bissett, and Dadswell 1950; Hopkins 1968), and many of the results presented here could be interpreted in terms of a competitive relationship between cambial activity and epicormic shoot production. Kramer (1964) lists the important requirements for cambial activity as a temperature suitable for a high level of metabolic activity; a supply of growth regulators, especially auxin; a supply of carbohydrates and nitrogen-containing substances; a supply of mineral nutrients; sufficient water to maintain cells in a turgid condition. The supply of many of these factors inhibited epicormic shoot production.

In the field also, the trees most likely to form epicormic shoots are those showing least cambial activity, i.e. the suppressed trees. Following thinning, epicormic shoots on the more vigorous trees are formed preferentially within the crown, on the upper bole, and on the more exposed sides. All these positions suffer greatest exposure and, possibly, dehydration inhibiting cambial activity.

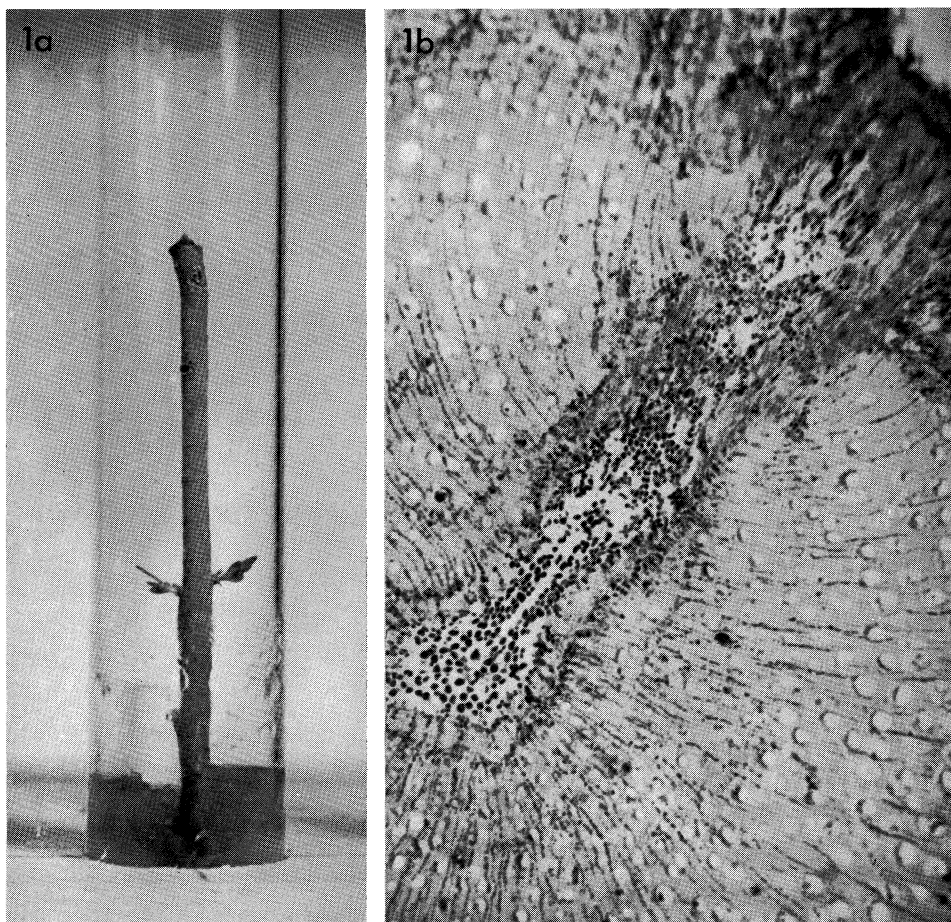


Fig. 1.—Production of epicormic shoots on isolated stem segments, showing growth of shoots (a) and their origin from dormant bud strands (b).

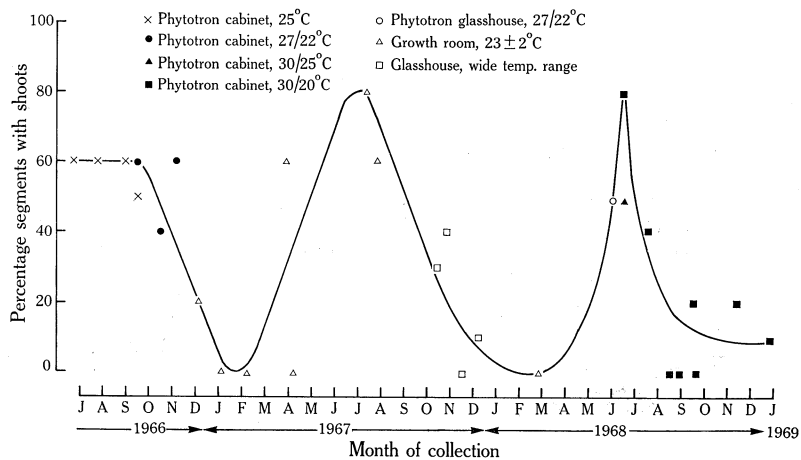


Fig. 2.—Variation in epicormic shoot production with time of collection of stem segments.

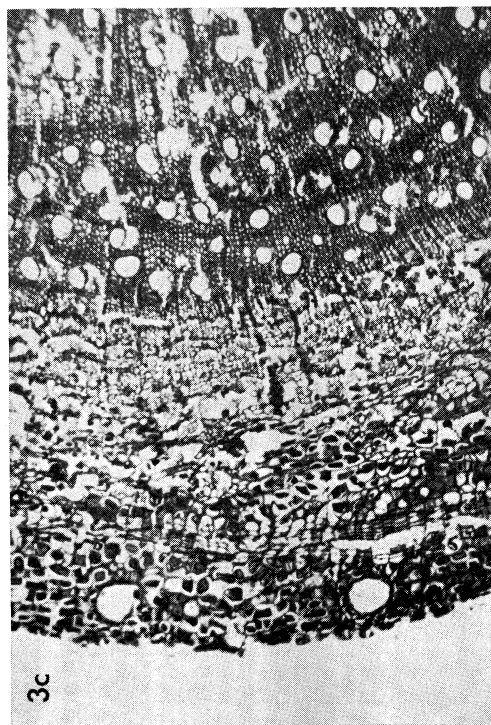
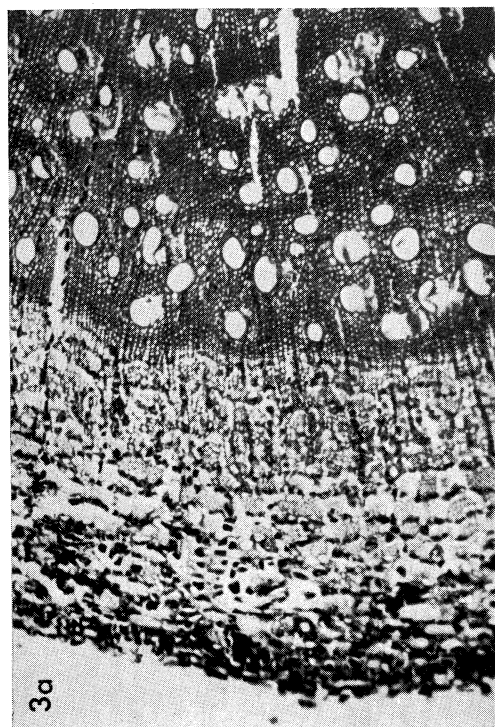
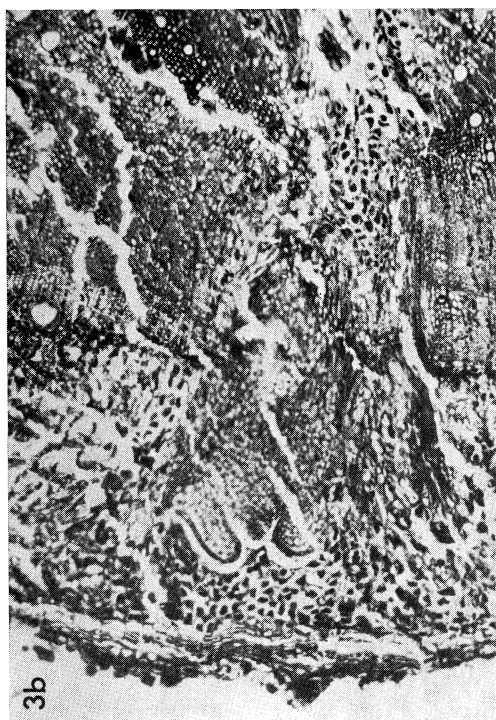


Fig. 3.—Effects of growth substances on bark cambial activity after 1 week of treatment. (a) Control. (b) Treated with IAA (10 mg/l)—showing position of epicormic bud and limited cambial activity. (c) Treated with IAA (10 mg/l) and GA_3 (10 mg/l).

The seasonal variation in epicormic shoot formation on isolated segments under controlled conditions could be interpreted in terms of an endogenous inhibitor produced, under short days, in sufficient quantities to inhibit cambial activity but not epicormic shoot development.

With these considerations in mind it was decided to test the effects of various inhibitors, in the presence and absence of growth substances, and to examine the effects of growth substances on cambial activity.

The metabolic inhibitors cinnamic acid, 2,4-dinitrophenol, and phenyl mercuric acetate at concentrations from 10^{-2} to 10^{-6} M and salicylic acid and coumarin at concentrations of 10^{-5} and 10^{-6} M all failed to stimulate epicormic shoot production on segments collected in summer. DL-Abscisic acid (50% *cis,trans* and 50% *trans,trans* isomer), an inhibitor now known in its *cis,trans* form to occur naturally in a wide variety of plant species (Milborrow 1967), likewise failed to give any real stimulation of shoot production when tested at concentrations from 0.05 to 1.6 p.p.m., in the presence or absence of GA₃ (1 and 10 p.p.m.) and IAA (1 p.p.m.), on segments collected in summer.

Since GA₃ appeared to be a particularly effective inhibitor of epicormic shoot production, the effects of the "antigibberellin"-type growth retardants 2-chloroethyl-trimethylammonium chloride and Amo 1618 were tested without effect.

Segments, collected in summer (January), were placed in media containing IAA (10 mg/l), GA₃ (10 mg/l), or combinations of these, and were situated in a shaded glasshouse. Segments were removed at intervals over a 2-week period after treatment, and the central portion sectioned to observe the effects of treatment on cambial activity. Auxin and gibberellin did not promote activity of the wood cambium, as observed for a variety of other species (Wareing, Hanney, and Digby 1964; Bostrack and Struckmeyer 1967), but they did appear to stimulate initiation and activity of a bark cambium. Development of this cambium was greatest in segments receiving GA₃+IAA, sometimes occurred in segments receiving IAA or GA₃ alone, and was not observed in control segments (Fig. 3). The position of this cambium is closely associated with the growing point of the epicormic bud—much more closely than the association between bud and wood cambium.

The results presented here show some interesting contrasts and similarities to those of Shapiro (1958) on the growth of root primordia in the stem of Lombardy poplar. Root primordia in Lombardy poplar are initiated during the first year of growth on any branch, grow radially outwards at the same rate as the diameter growth of the stem, and remain just inside the bark for the life of the tree. They are thus comparable in behaviour to epicormic buds. Shapiro (1958) found that the development of roots from the primordia was inhibited by white and by red light whilst blue and green lights had almost no effect. These results are almost the opposite of those on the effects of light wavelength on epicormic shoot formation, but the way in which light acts in either system is unknown.

Shapiro (1958) also found marked seasonal variation in root development, a variation which almost exactly paralleled the results given here. In his work, however, auxin at a concentration of 50 p.p.m. overcame this variation.

Auxin applied alone inhibited epicormic shoot formation but so too did a variety of other factors including GA₃, kinetin, nutrient supply, and high water

availability. The results from this study are consistent with a hypothesis that there is a competitive relationship between cambial activity and epicormic shoot production such that epicormic shoot formation is favoured at times when the cambium is dormant. Such a relationship could explain the experimental results given here, and also observations in the field.

Much of the evidence for this relationship is indirect, but the small amount of direct evidence suggests that a bark cambium may be of more significance than a wood cambium. This aspect of the work requires considerably more investigation.

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