

PHOTOPERIODIC EFFECT ON POLLEN SHEDDING IN
PINUS RADIATA?*

R. D. BURDON

Forest Research Institute, New Zealand Forest Service, Rotorua

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Adult material (grafts) of *Pinus radiata* D. Don was grown in a heated glasshouse for 19 months, starting from mid-winter. From mid-summer to mid-summer half the material was given continuous supplementary incandescent light and half kept in ambient photoperiod (Burdon, 1974). All material became largely disentrained from the normal seasonal growth rhythm, and in both treatments pollen cones started to become visible during spring instead of during late summer.

In the second summer the plants with unseasonably formed pollen cones were moved outdoors. However, there was virtually no pollen shedding from mid-summer until close to the normal pollen-shedding season in late winter, even from pollen cone clusters which had started dehiscing before this period. On some shoots two successive pollen cone crops had appeared several months apart but dehiscence at almost the same time (Fig. 1).

It appears certain that during autumn there was a powerful inhibition of pollen shedding by some factor or factors of the external environment. This prolonged inhibition could be explained in terms of an effect of decreasing photoperiod (cf. Jenkins *et al.*, in press.) rather than of absolute daylength or of any particular temperature regime.

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FIG. 1 (opposite)—Graft kept in glasshouse under ambient photoperiod until 6 January 1969, as at 13 June 1969. There are two successive crops of unopened pollen cones separated by a zone of fully elongated vegetative shoot. Pollen shedding in the lower crop appeared imminent by April but did not begin until 26 June 1969. (Photo — R. D. Burdon.)

* A detailed and illustrated account under the same title is available on request from the Editor.



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INTRODUCTION

Pinus radiata D. Don normally shows seasonal rhythms in its growth and reproductive processes, although this rhythmic pattern is less pronounced in the growth of juvenile trees. The formation of reproductive structures is closely related developmentally to many vegetative growth processes; for example, female strobili normally occur as part and parcel of branch clusters (Bannister, 1962). This undoubtedly imposes some parallels between the seasonal rhythms of growth and reproduction.

Regarding environmental factors which control the rhythms, temperature certainly has some effect, if only in a general slowing caused by low winter temperatures. Photoperiod has been shown to be capable of influencing shoot elongation (see Jenkins et al., ¹⁹⁷⁷ ~~in prep.~~). It does not, however, appear to impose strict dormancy, while its precise importance as a control in field conditions is not established. In the absence of strong seasonal differences in temperature, daylength, and water availability the species can fail to show an annual growth cycle while pollen shedding can occur at all times of the year (Lanner, 1966).

There has been no definite information on whether reproductive processes are subject to seasonal control over and above any such control of vegetative growth. Similarly, there has been little information on whether or to what extent successive stages of reproductive development are under independent environmental control. If the timing of reproductive processes is under any specific environmental control, rather than being strictly coupled with vegetative growth rhythms, there arises the question

of the roles of individual factors of the environment in exerting such control.

This report is specifically concerned with the dates of pollen shedding from pollen cones which had appeared unseasonably on material growing under glasshouse conditions. The cones appeared during a pilot experiment designed to study the effects of continuous light on vegetative growth (Burdon, 1974, Expt. 2), but the major interest for this report lies in whether pollen shedding was correspondingly unseasonable when the plants were kept in ambient conditions.

DEVELOPMENTAL PATTERN OF POLLEN-BEARING BRANCHES

The morphology and the normal developmental cycle of pollen-bearing branches of P. radiata are now outlined as a basis for evaluating the results of the study.

Pollen cones normally occur on shoots which are of low vegetative vigour. These shoots are mainly branches of at least the second order and, except in old trees, are concentrated towards the lower part of the crown. Such shoots are strictly monocyclic, showing only one cycle of shoot extension per year, unlike the leading shoots and major laterals of most trees.

The annual growth stage of such a shoot represents three well-defined zones. The lowest zone, only about 1 cm long, is characterised by cataphylls which do not subtend any axillary organs. At the base of this zone the cataphylls are in highly compressed parastichies, which provide the best clue to annual growth stages (Jacobs, 1937). In the middle zone, pollen cones occur in the axils of the cataphylls. The upper zone is characterised by having fascicles subtended by the cataphylls. At the very top of this zone long-shoot lateral buds may or may not be present, such buds giving rise to higher order branches of the next annual growth cycle.

Primordial development for a growth cycle is certainly well underway by the end of the spring preceding elongation of that cycle (M.P. Bollmann, pers. comm.). By summer there is a well-developed sealed bud, which progressively enlarges. It is not known, though, when pollen cone initials and fascicle initials are determined as such. By late summer to early autumn (generally early to mid-March in the Rotorua area) pollen cones become clearly evident externally, with the bud having a swollen zone which contains the cones and which subtends an obviously narrower vegetative zone. By mid-winter the microsporophylls are well emerged from the bract scales at the bases of the cones. At this stage the zone of the shoot which bears the pollen cones has largely completed its elongation, despite what Jacobs (1937 p.4, para. 5) has implied.

As dehiscence approaches, absolute enlargement of pollen cones is quite rapid. The actual pollen shedding occurs during late winter to early spring (i.e., late July to early to mid-September at Rotorua), and up to several weeks later on cooler sites than on warmer ones. The upper zone of the shoot shows limited stem elongation and almost no fascicle elongation until pollen shedding is completed.

EXPERIMENTAL AND RESULTS

All work was done at Rotorua, Lat. 38°S.

Phase 1 - December, 1967 to January 1969

Grafts, 25-40 cm tall, from 21-year-old trees were potted up and transferred into a heated glasshouse in June 1967. Temperatures in the glasshouse were nominally kept between 15°C and 24°C, but they occasionally exceeded 27°C.

From 21 December 1967 to 9 January 1969, the material was given two treatments in the glasshouse - continuous light (CL) and ambient photoperiod (Ambient). The CL treatment involved supplementary incandescent

light, ca. 4 Wm^{-2} , day and night. Since photoperiod was necessarily confounded with other effects the results of this experiment are reported here only insofar as they relate to the follow-up study during Phase 2.

In both treatments the presence of pollen cones became clearly evident on some of the plants at about the normal time of year (in early March). These pollen cones dehisced at a range of times (from May, with CL) before or up to the normal pollen-shedding season (in August). The plants became disentrained from a monocyclic growth pattern in that a flush of vegetative shoot elongation began during autumn, and the disentrainment became progressively more marked. This disentrainment was evident in shoots which, in respect of general vigour and the presence of pollen cones, resembled pollen-bearing branches of trees in the field. In the grafts which were growing in pots, however, these shoots were first-order branches and sometimes even leaders.

Associated with the disentrainment of the vegetative flushing rhythm was the appearance of pollen cones at anomalous times. Well before January 1969, some plants in both treatments were showing subsequent crops of pollen cones which were associated with later cycles of shoot growth than was the first crop. In CL this was first noted on 26 August 1968, and by 6 January 1969, 12 plants were involved. Pollen shedding from these later crops of pollen cones had begun in two plants by mid-October and in a total of six plants by 6 January. The pollen cones in this treatment shed pollen in slow acropetal succession within clusters. With the Ambient treatment subsequent crops of pollen cones also became evident, in three plants by 30 October and in a total of 11 by 6 January; but no pollen was shed during this period.

Phase 2 - January to September, 1969

From 6 to 24 January 1969 all plants remained under standard glass-house conditions. Through till March further pollen cones became evident, so that several grafts bore two successive crops of undehisced pollen cones which were separated by fully elongated zones of vegetative shoot.

On 24 January, 23 grafts (14 from Ambient and 9 from CL) were planted in the open nursery, with minimal root disturbance. No ill-effects of transplanting were observed. After planting, the grafts were inspected weekly for pollen shedding until mid-May, and then on every fine day until mid-September. The appearance of further crops of pollen cones was not systematically recorded, however.

The timetable of pollen shedding for each graft is shown in Fig. 1. Although the pollen cone clusters on some plants had become evident as long as 6 months before normal, there was almost no pollen shedding during this period until mid-June. Even in clusters which had started shedding before 6 January (Fig. 2) the shedding ceased almost completely until the approach of the normal shedding date.

Equally noteworthy were plants with two successive crops of undehisced pollen cones. In some of these plants the second crop had become recognisable at the very least 19 weeks after the first crop. Yet by mid-May the two crops were in remarkably similar stages of development (Fig. 3^{*}). The cones shown in the second crop, although considerably smaller than those in the first, were still at a very advanced stage. However, the dates of shedding in successive crops on the same plant never quite overlapped (Fig. 1). Towards the end, when temperatures were warmer, the shedding proceeded much more rapidly.

One clone was represented as six ramets and two others as two ramets each. However, there were no definite clonal differences in dates of pollen shedding in this situation.

* Fig. 3 = Fig. 1 in published short note

DISCUSSION

Pollen shedding was clearly delayed or even interrupted during the entire period from mid-January to about mid-June in 1969. This can hardly be attributed to transplanting shock or nutritional stress; Fig. 3 shows that a major delay occurred despite good vegetative vigour. It seems certain, then, that there was a powerful inhibitory effect of the external environment. That the inhibition was not quite absolute, as is evidenced by the very occasional cone dehiscing within clusters which had started shedding during Phase 1, makes it scarcely less noteworthy.

Admittedly, the dates of pollen shedding still bore some relationship to dates of pollen cone appearance, as is evidenced by the time difference between the dehiscence of successive pollen cone crops within a plant. Moreover, the older crops of pollen cones did dehisce ahead of the normal pollination season. In both cases the time difference was about 6 weeks. However, since this represented the coldest time of the year, it is considered that the length of this period reflected the slowing effect of low temperatures rather than large differences in stages of pollen cone development. The interpretation is supported by the fact that dehiscence of later crops of pollen cones, which occurred in warmer conditions, was completed in a small fraction of the time taken by the earlier crops.

The long delays in the dehiscence of well-developed pollen cones indicate that final development and dehiscence, as distinct from determination, is a process which requires some separate environmental cue or cues. That the delay in pollen shedding could be accompanied by elongation of the rest of the current shoot cycle and of most of the next cycle (Fig. 3), suggests that shedding is under environmental control which is both independent of and stricter than the control over vegetative growth. This would not, of course, preclude the vegetative and reproductive processes from showing parallel environmental responses.

* Fig 3 in Burdon (1997) NZ J. For Sci 7(2):214-5

Casual observation by the author suggests that receptivity of female conelets of P. radiata can be inhibited during late autumn in a similar manner to pollen shedding. The branch buds occurring in the same cluster as female cone buds can sometimes show considerable elongation during autumn, despite which the associated female conelets do not emerge to become receptive until the normal pollination season towards the beginning of spring.

There remains the question of the basis of environmental inhibition of pollen shedding. Lack of chilling in itself can be virtually ruled out, because shedding occurred during Phase 1 despite a long period in the heated glasshouse. Low temperatures, although doubtless causing some slowing in winter, cannot account for the inhibition during autumn. However, an obvious and consistent difference in conditions between late summer and autumn, when shedding was apparently inhibited, and late winter to early spring, when shedding occurred freely, is that daylength decreases before the winter solstice and increases after it. In this connection there is now some experimental evidence (Jenkins et al., ¹⁹⁷⁷ ~~in prep.~~) that vegetative elongation is inhibited by decreasing daylength and promoted by increasing daylength. On existing knowledge an effect of this sort would provide the simplest and most satisfactory explanation for the pollen shedding behaviour reported in this paper.

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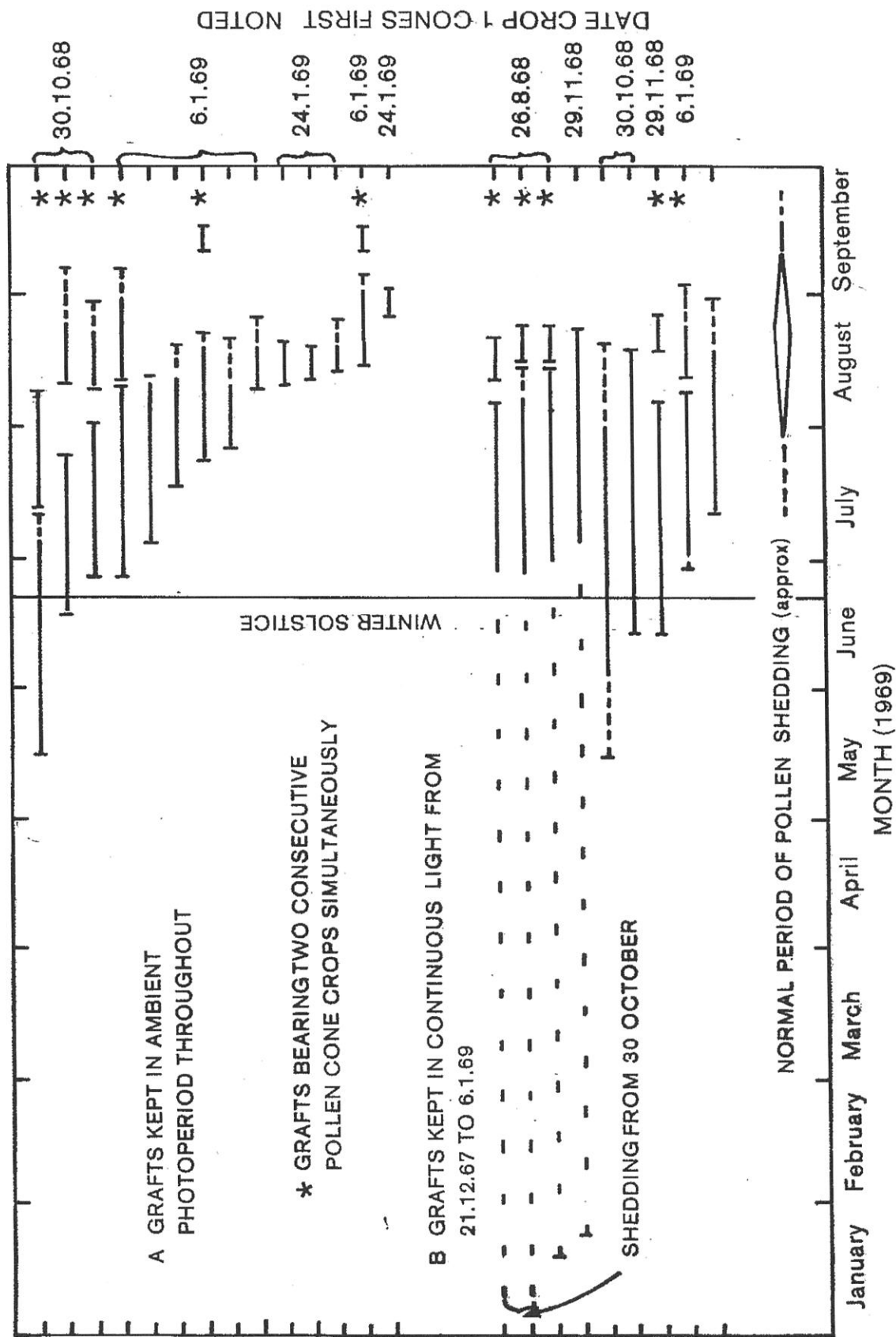


FIG. 1: TIMETABLE OF POLLEN SHEDDING IN GRAFTS AFTER PLANTING OUTDOORS ON 24.1.69
 Dashed lines indicate only very occasional cones shedding pollen. Dates of appearance of pollen cones are conservative, since pollen cones were often quite well developed when first recorded.

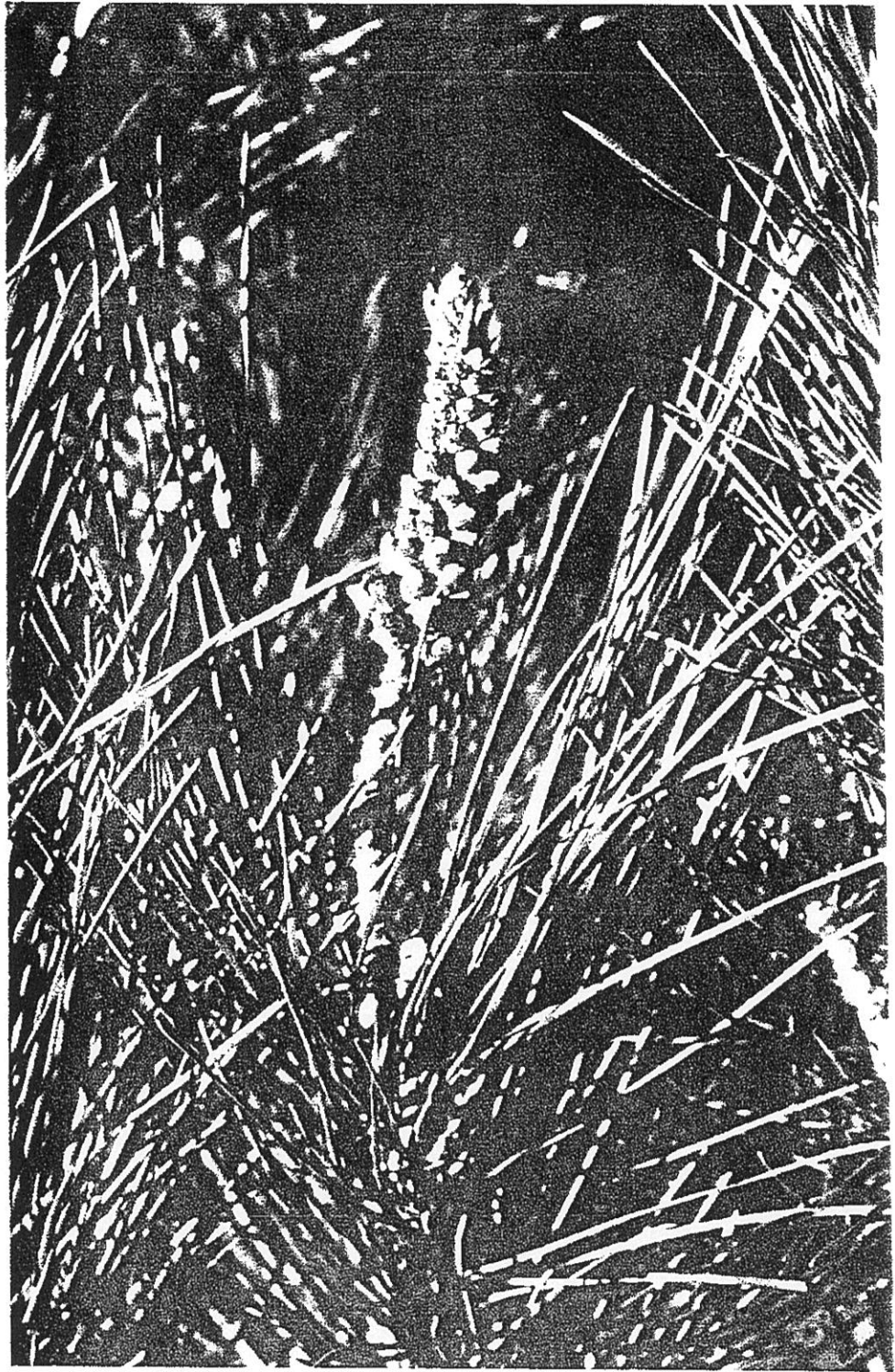


FIG. 2 - Partially dehiscent cluster of pollen cones, as at 13.6.69, in graft kept in continuous light till 6.1.69. Pollen shedding began at end of October, and virtually ceased from January till end of June 1969. Dehiscence of pollen cones has been followed by abscission, leaving the bare zone of stem below the undehiscent cones. (Photo - R.D. Burdon).