ENVIRONMENTAL CONTROL OVER THE SHOOT GROWTH OF PINE SEEDLINGS

S. Thompson[1]

Abstract.--In 1-0 Scots pine (*Pinus sylvestris* L.), shoot morphology and second season shoot growth potential are predetermined largely by date of budset and cessation of shoot elongation. They can be manipulated by photoperiod and temperature to produce seedlings of saleable size, uniform morphology and good potential for growth during their second season.

Résumé.--Chez le pin sylvestre (*Pinus sylvestris* L.) 1-0, la morphologie de la pousse et le potentiel de croissance de la pousse lors de sa deuxième année sont fortement prédéterminés par la date de la formation des bourgeons et de la cessation de la croissance des pousses. On peut influer sur eux en faisant varier la photopériode et la température pour produire des semis commercialisables, une morphologie uniforme et un bon potentiel de croissance pendant la deuxième année.

Through the use of containerized seedlings we can look forward to the day when planting survival is 100% and transplant shock no longer reminds us of how badly we have performed the transfer of the seedling from nursery to forest. Then it will be prudent to raise pine seedlings which, because of the high number of stem units (primordia) they hold at their apex, are predisposed to make good height growth during their first season in the forest.

The first season in the life of a north temperate pine is unique for it is the only time when the shoot growth of two seasons is determined by a single period of activity at the apical meristem. Consequently, the nurseryman has the ability to control 1-0 seedling height as well as the potential (based on the number of stem units held at the apex) for shoot growth during the seedling's first season in the forest.

The shoot apical meristem which produces the stem units for shoot elongation first becomes active during germination (Cecich and Horner 1977), but several weeks pass before shoot elongation starts. Until then the stem units are accumulated in the rosette (Thompson 1976). Under natural conditions the consumption of stem units in shoot elongation is outpaced by their production at the apical meristem so that the rosette is retained at the shoot apex throughout the first growing season. Shoot elongation ceases at budset and the seedlings then have the typical one-year-old shoot morphology (Type 1: Thompson 1981). This is characterized by the presence of a terminal rosette of primary needles at the centre of which is a bud of variable size. The stem bears primary needles with few axillary secondary needles. After a period of winter dormancy the stem units in the rosette and the bud elongate to form the second-year shoot (Thompson 1976).

When north temperate pine seedlings are raised outdoors, their first season height growth is limited by low temperatures, low soil fertility, moisture stress, etc. To reduce these limitations and produce seedlings of saleable size more quickly, many nurserymen have invested in structures within which the growing environment may be controlled to varying degrees (Tinus and McDonald 1979). When reared under increased temperatures and long photoperiods, seedlings of north temperate pines show increased rate of stem unit elongation. However, since stem unit consumption then outpaces stem unit production, budset occurs earlier; consequently, shoot growth ceases early and overall height growth

[1]Research Officer, Department of Forestry, University of Aberdeen, Old Aberdeen, Scotland.

is reduced. If they are retained in the same environment after budset these seedlings develop a shoot morphology similar to that of two-year-old plants (Type 2: Thompson 1981). This is characterized by the presence of a terminal resting bud (containing a series of structures similar to those of mature trees) with a whorl of lateral buds. Almost all the primary needles on the upper part of the shoot have axillary secondary needles which are of similar length.

If Type 2 seedlings are maintained in an environment in which growing conditions are not limiting the terminal bud will eventually flush, elongate the stem units it contains and then form another terminal bud. It is not known how long this recurrent flushing phase can be maintained. After 42 weeks with a 16-hour photoperiod and a minimum temperature of 21.1°C, Downs and Borthwick (1956) showed that Scots pine *(Pinus sylvestris* L.) of Swedish origin flushed twice, increasing their height by up to four times that at the end of the first shoot elongation period. In ponderosa pine *(P. ponderosa* Dougl.) recurrent flushing is the accepted mode of growth to obtain the desired height specifications for containerized seedlings (Tinus and McDonald 1979).

The thesis of this paper is that pine seedlings with a Type 2 shoot morphology, with or without recurrently flushed shoots, are biologically less desirable than those with a Type 1 one-year-old morphology. This conclusion is based on consistent results from several studies on Scots pine. Briefly, these studies have shown that shoot elongation started earlier, buds set earlier and shoot elongation ceased sooner in Type 2 seedlings than in Type 1 seedlings (Table 1). After one growing season Type 2 seedlings were shorter, retained fewer stem units for elongation in the second season but carried a greater foliage biomass than Type 1 seedlings. After two growing seasons, seedlings which had a Type 1 morphology remained taller than those which had a Type 2 morphology. We accept that this material has not been tested under forest conditions but it is predicted that the advantages held by the Type 1 seedlings will be maintained if not increased in subsequent years after outplanting.

Several workers have shown that shoot morphology in Scots pine seedlings can be modified by photoperiod (Wareing 1950, Downs and Borthwick 1956) and temperature (Denne 1971, Gowin *et al.* 1980). Similar studies have been carried out at Aberdeen to examine

Table 1. Differences in some components of shoot growth in Scots pine seedlings raised for 26 weeks in a heated, naturally lit greenhouse[a].

Parameter	Age (Years)	Sample No.	Shoot Type: Type 1	Shoot Type: Type 2	Significance level[b]
Seedling height (mm)	1	280	196	161	**
Seedling height (mm)	2	120	451	400	**
Weeks to budset	1	280	13.9	10.5	**
Stem unit number	1	280	135	104	**
Stem unit number	2	280	203	146	**
Stem unit length (mm)	1	280	1.13	1.19	ns
Stem unit length (mm)	2	120	1.38	1.75	**
Primary needle dry wt (g)	1	160	1.19	0.67	**
Secondary needle dry wt (g)	1	160	0.93	1.80	**

[a]See Thompson (1981) for more complete details
[b]ns - not significant; ** - significant at the $\alpha = 0.01$ level

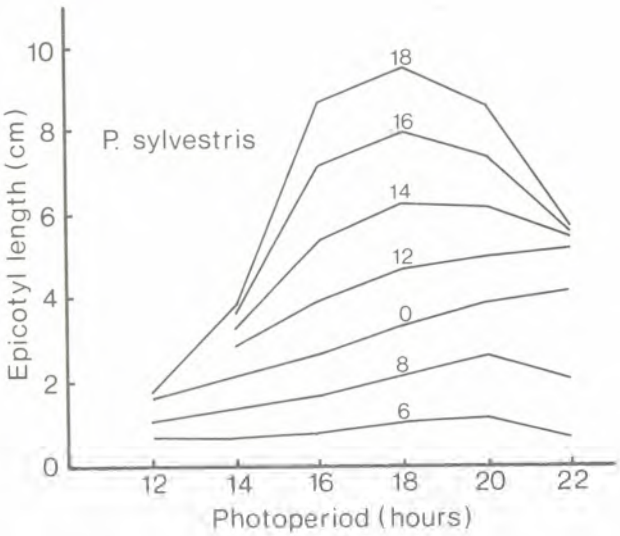

Figure 1. The effect of photoperiod on epicotyl length of Scots pine seedlings measured at 2-week intervals. (All plants received 12 hours of warm white fluorescent and incandescent light at a photon flux density of 95 mol m^{-2} s^{-1}. The photoperiodic supplements were provided by tungsten bulbs at a photon flux density of 6 mol m^{-2} s^{-1}. The day/night air temperature was 25/15°C).

more closely the effects of daylength and temperature on shoot morphology of Scots pine. When we repeated the work of Wareing (1950) we found that first season shoot elongation was most prolonged under a photoperiod of 18 hours and produced the tallest seedlings at 18 weeks after germination (Fig. 1). This was not so at 10 weeks when seedling height increased with increasing photoperiod (up to 22 hours). However, seedlings raised under a photoperiod of 22 hours had already set buds and in the following weeks they developed a Type 2 shoot morphology. At 10 weeks the seedlings raised under a photoperiod of 12 hours had also set buds but since stem unit elongation had also stopped they retained a Type 1 shoot morphology. At 18 weeks, 75% of the seedlings reared under a photoperiod of 18 hours had set buds but, since photoperiod was not limiting, shoot elongation continued to use up the stem units in the rosette. To retain Type 1 morphology a limiting factor must be introduced. Photoperiods of less than 12 hours' duration quickly induce the cessation of shoot elongation.

The effect of temperature on shoot growth morphology has also been studied. Under an 18-hour photoperiod, Scots pine seedlings were raised for 24 weeks from germination in 16 combinations of day and night temperature. At 8 weeks, for each day temperature treatment, epicotyl length increased with each increase in night temperature (Table 2). At 24 weeks, however, because of early budset under the 20 C night temperature treatments (Table 3), maximum seedling height in the day temperature treatments was at a night temperature of 15 C (Table 2). As in the photoperiod study above, shoot morphology was closely associated with time of budset. All the 20 C night temperature treatments, which had the earliest appearance of a terminal bud (Table 3), had high percentages of seedlings with a Type 2 or related shoot morphology (Table 4). Since no limiting factors were introduced during this experiment, many of the Type 2 seedlings, particularly in the 30/20 C day/night treatment, flushed their terminal buds. Some even flushed twice. The lack of limiting factors also allowed continued shoot elongation after budset in the Type 1 seedlings, which used up the stem units in the rosette. Although these seedlings produced many axillary secondary needles they did not develop the whorl of lateral buds characteristic of Type 2 seedlings.

Table 2. Epicotyl length as a percentage of the maximum attainable[a] in Scots pine seedlings raised under 16 day/night temperature combinations (n = 28).

Age (weeks)	Day temp. (°C)	Night temp. (°C) 5	10	15	20
8	15	14	19	36	52
	20	21	32	52	78
	25	28	42	75	100
	30	31	40	66	84
24	15	34	52	71	67
	20	45	68	89	70
	25	49	78	100	78
	30	58	86	100	68

[a]week 8 max = 31.9 mm; week 24 max = 131.9 mm

Table 3. Time to budset (weeks) for Scots pine seedlings raised under 16 day/night temperature combinations (n = 28).

Day temp. (°C)	Night temp. (°C) 5	10	15	20
15	16.6	17.1	14.1	11.8
20	14.5	14.8	13.5	9.9
25	14.9	14.1	12.4	9.2
30	14.6	14.4	14.4	9.1

Table 4. Percentage of Scots pine seedlings with a Type 1 or similar morphology at 24 weeks when raised under 16 day/night temperature combinations (n = 28).

Day temp. (°C)	Night temp. (°C) 5	10	15	20
15	100	96	80	31
20	100	100	82	15
25	100	100	79	19
30	100	96	81	7

From the evidence cited earlier it is clear that the production of Type 2 seedlings is undesirable and should be avoided. Therefore, nurserymen must develop rearing schedules that prevent the induction of early budset which would result if stem unit consumption and shoot elongation outpaced stem unit production by the apical meristem. Long photoperiods (the effect of interrupted nights has not yet been studied) and warm nights should be avoided. For the Scots pine source used in the above studies, seedlings about 15 cm tall with a Type 1 shoot morphology could be produced under a day/night temperature regime of 25/15°C with an 18-hour photoperiod until budset when a 12-hour photoperiod would be applied to stop shoot elongation. Different seed sources are likely to require different regimes to produce saleable seedlings. At Aberdeen, seedlings satisfying the same criteria can be produced in a greenhouse maintained at 25/15°C if the seeds are sown in late May and the naturally declining daylength is used to arrest shoot elongation (Thompson, unpublished data).

Clearly the same goal can be reached by different means. Difficulties will arise when nurserymen want to produce several crops in one year. Research is needed into methods of achieving dormancy and cold-hardiness that will ensure normal seedling growth in the second year, i.e., all apical stem units elongate to the same length as those of seedlings overwintered naturally outdoors.

The production of seedlings with a Type 1 shoot morphology will result in greater uniformity of product which will convey to the purchaser an impression of quality control. Type 1 seedlings, in addition to their greater second-season shoot growth potential, have a more uniform growth potential because they retain a continuum of stem units from the apical meristem to the base of the rosette. Type 2 plants lack synchrony when they start recurrent flushing (Downs and Borthwick 1956). Hence, when treatments are applied to stop height growth, the number of stem units at the apex will vary depending on the time elapsed since the previous flushing. The concept of "building a bud" must have evolved under such conditions. The uniformity of shoot growth potential in treatments which have greatly altered 1-0 seedling height (Thompson and Biggin 1980) suggests that this concept does not apply in the production of pine seedlings with a Type 1 shoot morphology.

Only when the problems of seedling survival and transplant shock have been overcome will the production of seedlings, which are predisposed to make good height growth during their first season in the forest, become a biologically and economically worthwhile objective. Through an understanding of the growth responses of pine seedlings to environmental inputs, the nurseryman will be better equipped to supply what the forester demands.

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