The Timing of Bud Set in Seedlings of Picea abies from Seed Crops of a Cool Versus a Warm Spring and Summer

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Abstract

Seedlings from bulked seed lots of 2 seed orchards from a cold (1987) and a warm (1989) seed year were tested for differences in bud-set in 8 controlled environment chambers and 3 nurseries. Seedlings of the 1987 seed lot formed terminal buds at shorter nights in growth chambers, and they formed buds earlier under natural day lengths in the nurseries, than seedlings from the 1989 seed lot. Time of flowering in spring was 17 days earlier in 1989 than in 1987 because of the mild winter and early spring of 1989. The results thus show that seed crops from different seed years may perform differently for adaptiv properties. It is suggested that night length and temperature during meiosis, pollination and fertilization and/or differences in temperature during the seed maturation period can affect the photoperiodic response of seed orchard progeny.

Key words: *Picea abies*, seed orchards, preconditioning, after-effects, bud-set, photoperiod, growth chambers.

FDC: 181.221.1/2; 165.5; 232.11; 232.311.3; 174.7 *Picea abies*.

Introduction

The photoperiodic response of spruce seedlings determines the timing of growth cessation in the autumn (Robak, 1957; Dormling et al., 1968; Magnesen, 1969; Heide, 1974) and to some extent the resumption of growth the following spring through its effect on the onset of dormancy in the autumn. In addition, the temperature modify the timing of growth cessation in autumn (Koski, 1985; Koski and Sievänen, 1985) and plays a major role in timing the flushing in the spring (Perry, 1971). Recent results with Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* (L.)) have shown that the parental environment, or more specifically the climate and weather conditions during sexual reproduction, may influence the adaptive properties of the progeny. Such effects have been observed after transfer of the parental clones from a northern to a southern latitude, from a high to a low elevation, or from an outdoor to an indoor climate in a greenhouse. The seedlings from the warmer environments have an extended growth period and a delayed development of frost hardiness in the autumn (Bjørnstad, 1981; Johnsen, 1988, 1989a and b; Dormling and Johnsen, 1992; Johnsen and Østreng, 1994; Lindgren and Wei, 1994; Skrøppa, 1994; Johnsen et al., 1994; Skrøppa and Johnsen, 1994). If progenies are affected by the weather during flowering and seed production, then a cold seed year should give hardier plants than a warm year even if the seeds originate from the same seed orchard. In Norway, large amounts of seeds were produced in 2 orchards in a cold (1987) and in a warm year (1989). The aim of the present study was to test whether seedlings from those 2 contrasting years respond differently to night length treatments. The results are discussed in relation to the differences in temperature and the time of flowering in the 2 seed years.

Materials and Methods

The seed lots

The seeds were collected in Lyngdal seed orchard located and the southern coast (58° N, 5 m to 50 m a. s.), and from the inland seed orchard, Opsahl, (61°30'N, 190 m to 230 m a.s.) in the years 1987 and 1989. The seed samples were taken from commercial collections (the State Forest Seed Station of Norway). Seeds were thus collected from all clones bearing cones. There were abundant flowering both years and the majority of clones had female flowers. The clones in the Opsahl seed orchard originate from higher altitudes (600 m to 800 m) in the south-eastern part of Norway. At Lyngdal the seeds were collected from 3 separate and well-isolated compartments Dale, Nyland, and Epledal within the seed orchards area. The Lyngdal seed orchard area consists of small patches of former agriculture land. The different compartments are separated by hills with more or less shrubby broad leaf trees. Spruce does not occur naturally in this region, and no stands have been planted near the seed orchard. Even though no pollen catchments have been done, pollen contamination from outside the seed orchards seems very unlikely (Johnsen et al., 1989). The clones in the compartments originate from different regions in the central and northern parts of Norway (63 °N to 66 °N). *Table 1* gives further details of the clones and the 2 seed orchards and the separated compartments of Lyngdal seed orchard. *Table 2* shows germination and seed weight for the different seedlots used.

Table 1. — Location and composition of the seed orchards.

SEED ORCHARD	COMPARTMENT	AREA HA.	NUMBER OF CLONES	ORIGIN OF CLONES
LYNGDAL 58°N	NYLAND	25.6	175	63°-65° N 100-250 m
LYNGDAL 58°N	EPLEDAL	7.5	50	65°-66° N 70-200 m
LYNGDAL 58°N	DALE	1.2	33	65°-66° N 200-450 m
OPSAHL 61°30'N		9.2	77	60°-62° N 600-800 m

Table 2. — Germination percentage after 11 days (germination speed; GS), germination percentage after 21 days (GP) and seed weight (SW) of 1000 seeds.

SEED ORCHARD	COMPARTMENT	COLLECTION YEAR	GS (%)	GP (%)	SW (g)
LYNGDAL 58°N	NYLAND	1987 1989	91 83	95 92	5.85 6.56
LYNGDAL 58°N	EPLEDAL	1987 1989	92 86	94 94	5.84 6.54
LYNGDAL 58°N	DALE	1987 1989	77 95	90 98	5.40 6.62
OPSAHL 61°30'N		1987 1989	75 75	93 95	5.92 5.87

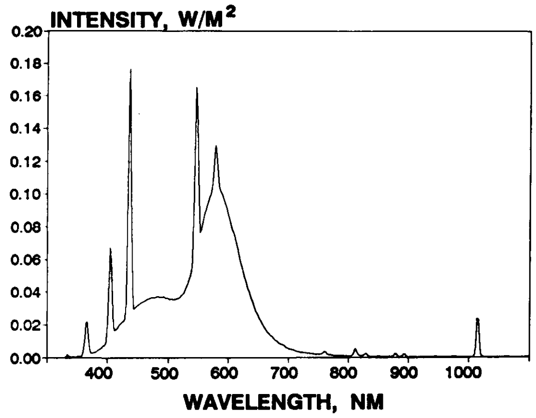

Fig. 1. — The spectral distribution of the fluorescent tubes in the growth chambers. The total flux ranged from 87 μmolm$-^2$s$-^1$ to 91 μmolm$-^2$s$-^1$ among the chambers.

The tests were conducted at the State Forest Seed Station of Norway in accordance with the ISTA (1993) regulations.

Meteorological data and time of flowering

No temperature records were specifically available from the seed orchard sites, so instead, Norwegian Meteorological Institution reports from weather stations located nearby the orchards were used to show the differences in mean temperature from January to August in 1987 and 1989. Mandal (21 km east of Lyngdal) and Lillehammer (30 km south of Opsahl) were the weather stations closest to the respective seed orchards.

Time of flowering was recorded both years at Lyngdal, but only in 1989 at Opsahl. The grafts at Lyngdal started to shed pollen on May 19 in 1987 and on May 2 in 1989. Pollen shed started on May 20 1989 at Opsahl. In both seed orchards the maximum pollen shed occurred 2 to 3 days later based on visual observations.

Experiments and assessments

Growth chambers with photoperiodic control

Seeds were sown in sphagnum peat mixed with 25 % perlite in multipot containers of the type Vefi 240. The container consists of 12 x 220 pots with a volume of 12 ml per pot. The seedlings were irrigated and fertilized in such a way that the containers were soaked every second or third day in a complete nutrient solution based on the commercial fertilizer Blue Superba with 13 % N — 4 % P — 19 % K — 1.5 % Mg with micronutrients. With 1 g/l it gave a conductivity of 1.2 mS/cm to 1.3 mS/cm.

The seedlings were grown in 8 controlled environment chambers with 1 chamber per photoperiodic treatment. The material was treated with night lengths ranging from 3 to 10 hours in 1 hour increments. The lighth source in each chamber was 3 fluorescense tubes (Osram 36W20 White with spectrum and intensity given in *figure 1*. The total flux (400 nm to 700 nm) ranged among chambers from 87 μmol m^{-2}s^{-1} to 91 μmol m^{-2}s^{-1}. The day temperature were between 22 °C and 23 °C, and the night temperatures were close to 21 °C.

The experimental design was randomized complete blocks. Each seed lot (*Table 1*) was represented by 4 to 6 seedlings per pot, a row of 12 pots per replicate, and was replicated 4 times within each chamber.

Most seeds started germination 5 days after sowing. A seedling was classified with (1) or without (0) a visible terminal bud 6 weeks from sowing. A few late germinating individuals which had not yet developed buds and secondary needles were excluded from further analysis.

Nursery trials

Seeds were sown in greenhouses at 3 forest nurseries in June 1992; Buskerud (59 °46'N), Skjerdingstad (63 °15'N) and Stiklestad (63 °48'N). Plants were kept in the greenhouses throughout the season and apart from occasional additional heating during the germination period, the temperature regime followed the natural fluctuations ranging from a maximum of 30 °C in mid summer to a minimum of 0 °C at the end of the experimental period. No additional light was applied. Multipot containers (M95), with a size of 40 cm x 30 cm x 8 cm and with a volume of 50 ml per pot, were used. The medium was sphagnum peat mixed with 25 % perlite. The plants were watered and fertilized with a complete nutrient solution (60 % Pioner Hornum macro and micro and 40 % $(NH_4)_2SO_4$)). This mixture gives a relative content for the macronutrient like N=100, P=13.9, K=72.6, Mg=17.3 and the conductivity is kept between 1.2 ms/cm to 1.5 mS/cm with 1.2 g/l to 1.5 g/l. In the beginning of August the N/K proportion was reduced by using only Pioner Hornum macro and micro giving a conductivity of 0.6 mS/cm to 0.8 mS/cm. The relative values of the macronutrients are then N=100, P=29, K=159 and Mg=36.5.

Each seedlot was represented by 1 to 3 plants per pot, 1 container per replicate, and replicated 4 times in the greenhouse.

Bud-set was recorded from August 19 to October 13. During registration containers were lifted to a table, plants were classified with or without a visible terminal bud, and then the containers were placed back to the same positions.

Statistical analyses

Experiments in growth chambers

The proportions of plants with terminal buds, were with the NLIN procedure (SAS Institute Inc., 1989), fitted to a logistic model (REHFELDT, 1977):

$$Y_{ijkl} = 1/(1 + ae^{-bXk})$$

which is represented by the linear model

$$\ln(1/Y_{ijkl} - 1) = - bX_k + \ln(a)$$

where

Y_{ijkl} = the proportion of plants with terminal bud in seed year i, seed lot j, and replicate l within night length k.

X_k = night length in the growth chambers

The constants a and b determine when (at which night length) the curves start to increase (a) and the rate of increase in proportions associated with an increase in night length (b).

The night length when 30 %, 50 % and 70 % of the plants had terminal buds (NL_{30}, NL_{50}, and NL_{70}) was calculated for each combination of seed year, seed lot, and replicate based on the a and b parameters from the fitted curves:

NL_{30}= (ln(a) — ln(1/0.3—1))/b

NL_{50}= ln(a) /b

NL_{70}= (ln(a) — ln(1/0.7 — 1))/b

NL_{30}, NL_{50}, and NL_{70} were subjected to statistical analyses with the procedure GLM in SAS to test the difference between the seed years by F-tests. Analyses were performed for each seed lot (Dale, Epledal, Nyland and Opsahl) separately, and a pooled (all seed lots together) analysis was performed as well. Seed year and seed lot were regarded as fixed effects and replication as a random effect. In separate analyses the residual was used as the error term,

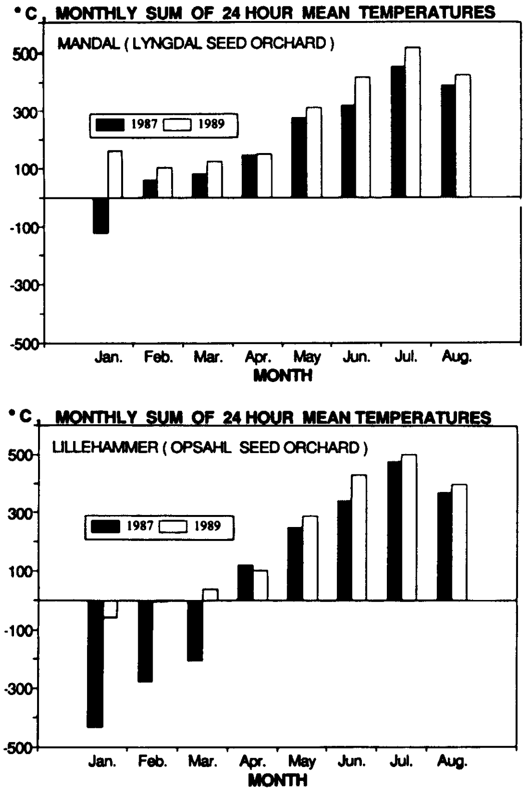

Fig. 2. — The accumulated 24 hour mean temperatures for the Norwegian Met. Inst. weather station Mandal / Lyngdal seed orchard at the south point of Norway (58° N) and for the Norwegian Met. Inst. weather station Lillehammer / Oppsahl seed orchard in central east Norway (61° 30' N) from January to August in 1987 and 1989.

and in the pooled analysis the interaction between seed year and replicate was used as the denominator when testing the difference between seed years.

Nursery trials

The proportions (p) of plants with a terminal bud were analysed for the dates when 20 % to 80 % of the seedlings from the seed lots had developed a visible terminal

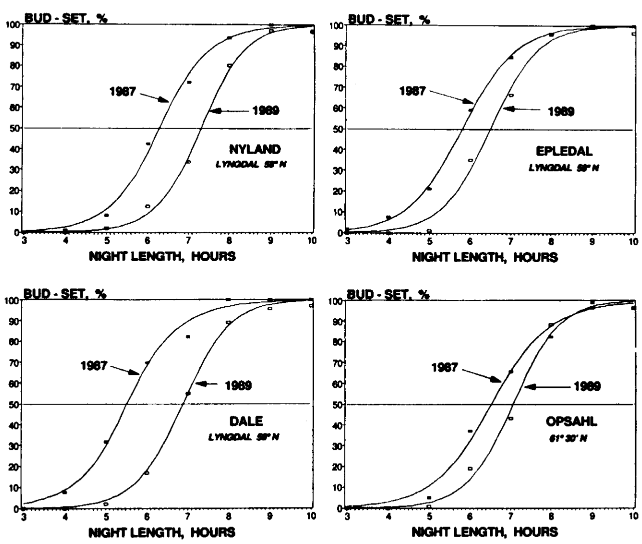

Fig. 3. — The photoperiodic bud-set response for the seed lots obtained from the separate compartments Nyland, Epledal and Dale at Lyngdal, and at Opsahl seed orchards.

Table 3. — p-values for the differences in bud-set between the years 1987 and 1989. NL$_{30}$, NL$_{50}$ and NL$_{70}$ are the night lengths when 30 %, 50 % and 70 %, respectively, of the seedlings had set terminal buds in the growth chamber experiment.

Seedlots	NL_{30}	NL_{50}	NL_{70}
LYNGDAL S.O. NYLAND	0.0217	0.0005	0.0009
LYNGDAL S.O. EPLEDAL	0.0085	0.0129	0.0301
LYNGDAL S.O. DALE	0.0026	0.0029	0.0098
OPSAHL S.O.	0.0217	0.0905	0.2790
Pooled analyses	0.0019	0.0016	0.0026

bud (September 1 or 2). Proportions were analysed both directly and after transformation to arcsine ($p^{1/2}$) with the GLM procedure in SAS. Differences between seed years were tested with F-tests obtained from separate analyses of each seed lot and nursery, of each nursery with all seed lots included, of each seed lot with all nurseries included, and finaly a total analysis with all factors included. Seed year, seed lots and nursery were fixed and replication within nursery was random. When testing the difference between seed years, residuals were used as error terms in separate analyses. However, when all seed lots were included in the analyses, the interactions between seed year and replicate within nursery were used as the error terms.

Results

Mean temperatures

The temperature was much higher in 1989 than 1987 in both seed orchards, especially during winter and spring, but also during summer and early autumn (*Fig. 2*). At Lyngdal the daily accumulated mean temperatures reached 1000 on July 6 in 1987 but the same value was reached as early as June 5 in 1989. This resulted in a 17 days earlier time of pollination at Lyngdal in 1989 than in 1987.

Growth chamber experiment

Differences were found in night length responses between the commercial seed lots produced in 1987 and 1989 (*Fig. 3*). The difference in NL$_{50}$ varied from 0.5 h to 1.3 h. The greatest difference was found at the compartment Dale in the Lyngdal area and the smallest one was found in the inland seed orchard of Opsahl. The analyses of variance revealed significant difference in NL$_{30}$, NL $_{50}$, and NL$_{70}$ for all seed lots from Lyngdal. For the seedlings from Opsahl significance was found for NL$_{30}$ only (*Table 3*). The pooled analyses (all seedlots included) confirmed that seedling from 1987 terminated their growth at significantly shorter night lengths than seedlings from 1989 (*Table 3*).

Nursery experiments

Similar differences between seedlots produced in 1987 and 1989 were also present in the nursery experiments. Seedlings from 1987 produced terminal buds earlier than those from 1989 (*Fig. 4*), and pooled analyses of variance including all the 3 nurseries showed significant differences in bud-set on September 1 for each seed lot (*Table 4*). The differences between years were more pronounced for Lyngdal than for Opsahl (*Fig. 4* and *Table 4*), and confirmed the results from the chamber experiments. The p-values of tests of difference in bud-set between 1987 and 1989 from separate analyses (single combinations of seedlot and nursery) were less than 0.05 in 7 out of 12 indi-

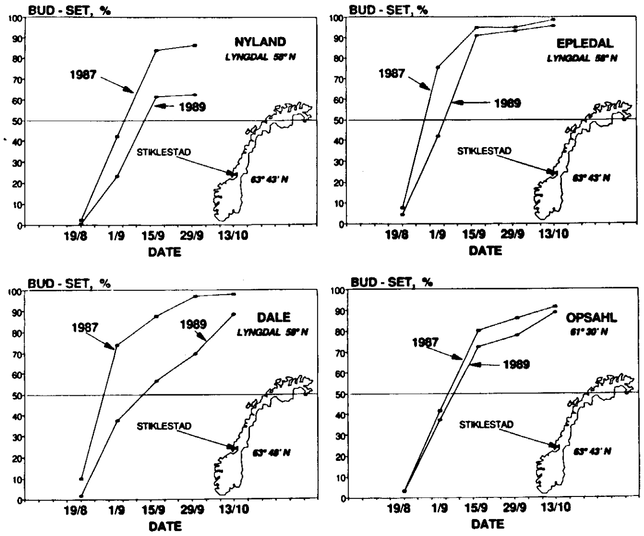

Fig. 4. — The bud-set development in autumn at Stiklestad nursery for the seed lots obtained from the separate compartments Nyland, Epledal and Dale at Lyngdal and at Opsahl seed orchards.

Table 4. — p-values for the differences in bud-set on September, 1 between the 1987 and 1989 seed lots. Analyses for each seedlot. locality, compartment and total analysis over compartment and locality.

Seedlots Nursery	NYLAND LYNGDAL	EPLEDAL LYNGDAL	DALE LYNGDAL	OPSAHL	Pooled
BUSKERUD 59°46' N	0.0228	0.0234	0.072	0.0241	0.013
SKJERD.STAD 63°15' N	0.0726	0.1130	0.0016	0.6099	0.025
STIKLESTAD 63°48' N	0.0253	0.0053	0.0199	0.3655	0.001
Pooled	0.0004	0.0005	0.0001	0.0305	0.0001

vidual cases, and were less than 0.025 in the pooled analyses (*Table 4*).

Discussion

Effects of the weather during sexual reproduction

We hypothesize that the difference between seedlots produced in 1987 and in 1989 was mainly caused by the differences in weather in the 2 seed years. Temperature during the winter and early spring of 1989 at Lyngdal (*Fig. 2*), resulted in a 17 days earlier flowering than in 1987 and probably earlier flowering at Opsahl as well. The prezygotic stages and fertilization thus occurred under more than 1 h shorter photoperiod in 1989. Accumulated daily temperature during embryo development and the seed maturation period were also higher in 1989. The results suggest that temperature and photoperiod during pollination, fertilization and embryo development may have significant effects on progeny performance of spruce. These effects should be further investigated. Possible mechanisms for such effects have been discussed in other papers (Johnsen, 1989a; Skrøppa and Johnsen, 1994; Johnsen et al., 1994).

At Lyngdahl in 1987 and Opsahl in 1989 the flowering took place on corresponding dates. The differences in bud set curves for these 2 seed lots reflects the genetic differences between the parental material in the 2 seed orchards (*Table 1*).

Possible effects of seed weight, seed size and germination properties on bud-set can hardly explain the large difference between seedlings from 1987 and 1989. Although the seeds from the Lyngdal seed orchard were heavier in 1989 than in the 1987 crop year, no difference in seed weight was found at the Opsahl seed orchard (*Table 2*). Initial differences in seed weight and size might account for a portion of the variation in seedling size, both after the first and later growth seasons (Perry, 1976), but seed weight apparently does not affect the bud-set of first year seedlings of Norway spruce (Skrøppa, 1988). An increase in seed weight due to the warmer climate in a southern seed orchard could not explain the more southern photoperiod response of the northern seed orchard progenies (Johnsen, 1989a; Johnsen and Østreng, 1994; Skrøppa and Johnsen, 1994). The hypothesis that heavier seeds could give rise to less frost hardy seedlings, has also been rejected by Johnsen et al. (1994). Seed quality traits other than seed weight could affect progeny performance (Ellis, 1992). However, both germination speed and percentages showed inconsistent differences between seed years among the seed lots (*Table 2*). Although germination speed was faster in 1987 for Nyland and Epledal, and slower for Dale, no difference between years was found for Opsahl. Germination percentages were similar in each of the 2 years, except for Dale where the germination percentage was significantly ($p=0.05$) higher (8%) for the seeds produced in 1989.

It is unlikely that a possible slight change from 1987 to 1989 in parental contribution to the seed crop could account for the clear differences in bud-set between seed years. Flowering was abundant in both orchards in both years, and many clones as well as many individual grafts of the clones produced seeds both years. The Lyngdal seed orchard is located on a site well isolated from outside pollen sources. The nearest natural spruce stand is located 20 km north of the orchard, and the predominant wind direction is from south-west. Moreover, we have data showing that control- and open-pollinated progenies from the Epledal compartment of the Lyngdahl orchard do not differ in autumn and winter hardiness (Johnsen et al., 1989), a result which supports the argument that pollen contamination is negligible in this orchard. Thus, differences in background pollination cannot explain the differences in bud-set between 1987 and 1989 seed crop from this orchard. Pollen contamination could on the other hand be a significant factor at Opsahl seed orchard. At Opsahl the difference in bud-set in the years 1987 and 1989 was less pronounced, however, which indicates that pollen contamination cold reduce rather than enhance crop year differences.

Practical implications

All 1989 seedlots produced seeds and seedlings which demonstrated a more southern or lowland performance with respect to bud-set than seedlots produced in 1987. A night length difference of 1 h measured in the degree of bud-set of seedlings grown in climate chambers (*Fig. 3*) is of the same magnitude as the bud-set differences seen between provenances from 66 °N and 63 °N, and between provenances from 700 m and 500 m in southern Norway (Kohmann, unpublished). These differences are of practical importance, and trials are in progress to test whether the differences of photoperiodic response are transitory or persistent. Recent reports indicate than the effects of the parental environment on progenies could last for many growth seasons (Johnsen, 1989a and b; Johnsen et al., 1989; Lindgren and Wei, 1994; Skrøppa, 1994). If true genetic differences are expressed, they could be transmitted to the next generation as well.

Acknowledgement

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Screening Pinus sylvestris for Resistance to Sphaeropsis sapinea

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Summary

Artificial inoculation was used to determine if it is feasible to screen for resistance to *Sphaeropsis sapinea* (FR.) DYKO and SUTTON in 2-year old seedlings of *Pinus sylvestris* L. Six varieties were exposed to 2 spore concentrations in outdoor mist chambers. Inoculations were repeated on 4 dates in late spring to early summer.

Varieties differed in infection incidence, indicating potential resistance. Phenological growth stage of seedlings was more important than date of inoculation; infection levels decreased after needles began to elongate. Therefore inoculations would be most effective during active shoot elongation prior to needle elongation. At least 2 inoculations are recommended when screening for resistance with this method because the incidence of infection varied among growth stages, and varieties differed in growth periodicity.

The Penn State XP-74 variety was found to be more resistant than the others, and the East Anglia variety was the most susceptible after varietal infection rates were adjusted for variation due to stage of growth and health of seedlings. The evidence for resistance suggests that genetic improvements may be attained through this screening method.

Key words: Pinus sylvestris, Sphaeropsis sapinea, Diploida pinea, disease resistance, selection method.

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Introduction

Sphaeropsis sapinea (Fr.) DYKO and SUTTON (=*Diploida pinea* [DESM.] KICKX.) causes a variety of diseases including seedling collar rot, tip and twig blight and, on weakened or injured trees, stem cankers and stem and branch dieback. Conifers in eight genera are susceptible to this fungus, but it is most common in *Pinus*. Pycnidia can be found singly or in clusters on bark, cone scales, and leaves. Conidia initially are yellowish-brown, darken with maturity, and occasionally are uniseptate (HADDOW