Relationship between development of *Larix decidua* seed cones and the time of colonization by insects

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ABSTRACT

Over a period of five years, the most destructive insects of *Larix decidua* Mill. (Pinaceae) cones and seeds produced in a seed orchard situated at Hemeiusi-Bacau, eastern Romania, were *Resseliella skuhravyorum* Skrzypczyńska (Diptera: Cecidomyiidae), *Strobilomyia melania* (Ackland) and *S. infrequens* (Ackland) (Diptera: Anthomyiidae), and *Retinia perangustana* (Snellen) (Lepidoptera: Tortricidae). *Strobilomyia laricicola* (Karl) and *Dioryctria abietella* (Denis & Schiffermüller) (Lepidoptera: Pyralidae) were less frequent. The relationships between the phenology of seed cones and of the most destructive insects were also studied. Temperature sums accumulated until specific phases of cone development and insect stages were calculated for the entire study period and used to estimate degree-day requirements above a threshold value of 5 °C for these events. Predictions of the beginning of oviposition and hatching of these pests were accurate and could be used to time control operations, if necessary.

Pages 157-172 in Battisti A, Turgeon JJ (eds). 1997. Proceedings of the 5th Cone and Seed Insects Working Party Conference (IUFRO S7.03-01), September 1996, Monte Bondone, Italy. Padova: Institute of Agricultural Entomology, University of Padova.

INTRODUCTION

The biological cycles of insects exploiting cones and seeds of conifers, especially those of conophytes, is typically synchronized with the production and the development of seed cones. For some coniferous trees, including those of the genus *Larix* (Pinaceae), morphologically recognizable phases of development at which cones are infested by insects have been identified (Roques 1983, 1988a, b, c, 1989; Olenici 1990; Yao *et al.* 1991; Turgeon & de Groot 1992).

It is critical to identify these phases to gain a better understanding of the way insects recognize and select the cones using specific visual and olfactory cues (Roques 1986, 1987, 1988a; Yao *et al.* 1991; Jenkins & Roques 1993; Roques *et al.* 1995), and, from a more practical perspective, to gain predictive knowledge of the time insect attack occurs. Such knowledge is critical for the management of cone crops because the time events such as pollen- and seed-cone bud burst, pollination, cone growth and elongation, seed maturation and insect attack occur, differ among years and sites (Leven 1951; Roques *et al.* 1984; Amirault & Brown 1986; Olenici 1990), mainly because of differences in weather conditions. The development of an integrated pest management system for seed orchards necessitate a simple method to identify when such events take place. Thus, it would be very useful to identify specific phases of cone development and the period of attack for each of the insect species infesting seed cones in relation to these phenological phases and calculate the degree-day requirements for such events. This information could be especially useful in remote seed production areas where access is difficult or in those where adequately-trained personnel required to monitor cone production and survival throughout its development, is in short supply.

The purpose of this research was to estimate the degree-days requirements for the various phases of *L. decidua* seed cone development and for the time of attack by several insect pests associated with this resource.

MATERIALS AND METHODS

Study Site. This study was carried out in a 5.6 ha seed orchard of *L. decidua* located at Hemeiusi-Bacau (46°35' N, 26° 58' E; 180-200 m). All important pests of cones in this orchard had already been identified (Olenici 1990, 1991, 1998). Population levels of these pests were considered high enough that changes in seasonal trends of populations could be detected with small sample sizes.

Dynamics of cone growth and temporal distribution of insects. Cone growth was studied by selecting in 1991 five trees of the same clone. These trees produced few flowers in 1992 and in 1995. Thus, in these years we had to select more trees, but all from the same clone.

Seed cones were collected each year from late-March/early-April until late-June/early-July. Cone sampling generally took place once a week, although occasionally it occurred at 10-14 d intervals. At each sampling date, 10 seed cones per tree were collected from the mid-crown and observations on the phenology of the cones were made simultaneously. Such observations were more frequent at the beginning of seed cone development. The sampled cones were analysed soon after collection or were placed in plastic bags and frozen until dissection. The length and maximal diameter of each cone as well as the aspect in which these reproductive structures had been sampled were recorded. The length of five ovuliferous scales, only three in 1995, from the zone of maximum diameter and the length of the corresponding bracts were also measured.

All cones were dissected under a stereo-microscope and the number of eggs and larvae of each species was recorded. The eggs of all species of *Strobilomyia* were identified on the basis of their position on the cone (Roques *et al.* 1984). Larvae could also be identified but only for a short time after egg-hatch if larval densities per cone were low and if larvae were close to the eggshell. Cone damage was also recorded for each species or group of species, as was the case for *Strobilomyia*. When the cone axis was damaged by a *Strobilomyia* larva, it was assumed to be *S. laricicola* (Roques 1983; Roques *et al.* 1984).

Sometimes, especially at the beginning of egg-hatch, only eggshells were found within the cones. In such cases we considered that the larvae had hatched, because it was too early for egg parasites to develop and to leave the eggshells.

Table 1. **Monthly mean temperature and the number of degree-days accumulated 60 d after the beginning of the year (01 January) at Hemeiusi-Bacau, Romania, 1991-1995**

	Mean temperature (°C)						Degree-days
Year	**January**	**February**	**March**	**April**	**May**	**June**	**(°d)†**
1991	-0.6	-3.1	3.7	9.3	12.7	18.6	17.5
1992	-1.7	-0.6	4.4	9.6	14.0	18.4	24.2
1993	0.0	-1.8	0.8	8.4	16.8	19.0	50.3
1994	1.9	-0.5	6.2	11.6	16.7	18.8	38.9
1995	-3.1	4.0	4.6	10.4	14.1	20.4	65.7

† Threshold value of 5°C

The mean number of eggs and larvae per cone was calculated for each sampling date, first for each tree and then for all trees. Because the number of *Strobilomyia laricicola* eggs was low and because the eggs of *S. melania* and *S. infrequens* were laid at the same time, both the mean number of eggs and of larvae per cone were combined for the three species. For *Resseliella skuhravyorum,* the mean numbers of eggs on 07 May 1992 (Tree 4), and of larvae on 11 May 1993 (Trees 2, 3) were abnormally low. It is possible that on these dates, cones from these trees were collected from the lower crown, where densities per cone are lower than in the mid-crown (unpubl.). To avoid artificial changes in the trends of population density, results from these trees were not included in our analyses for those years. Also data analyses for 1995 are based on only three trees because data for the other two are currently being processed.

Calculation of degree-days. The meteorological data necessary for this study were obtained from the Bacau station located approximately 10 km away from the seed orchard. There is no orographical obstacle between the weather station and the seed orchard that could cause significant changes on the main climatic parameters between the sites.

Estimates of degree-days (°d) above 5°C were calculated starting on 01 January (Julian date – JD 1) from maxima and minima using the algorithm developed by Morris & Bennett (1967), and published by Frazer & Gilbert (1976).

The model explaining the influence of temperature on cone and insect development was developed by comparing the intervals of degree-days at which each phenological phase or stages occurred each year. As the time between some observations was rather long, it was assumed that each phase occurred between the latest beginning and the earliest ending recorded for that phase.

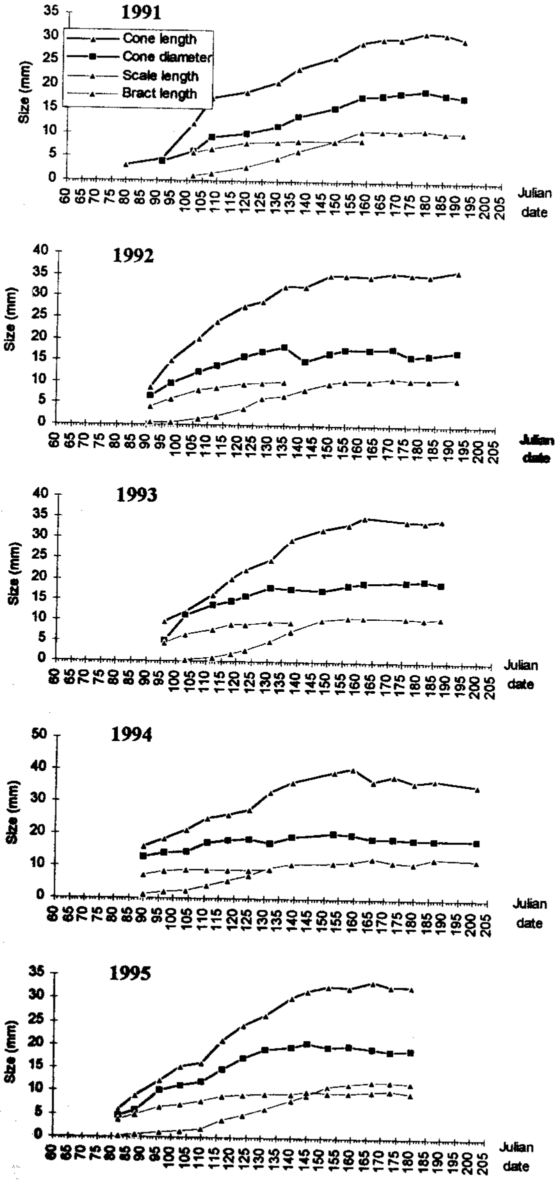
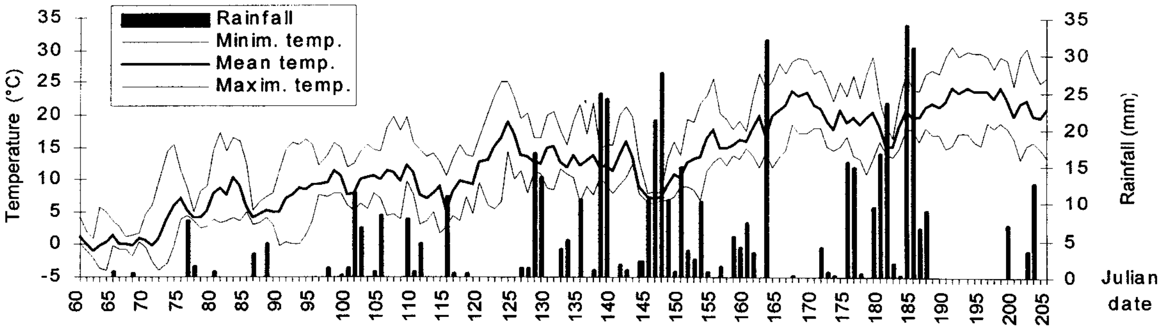


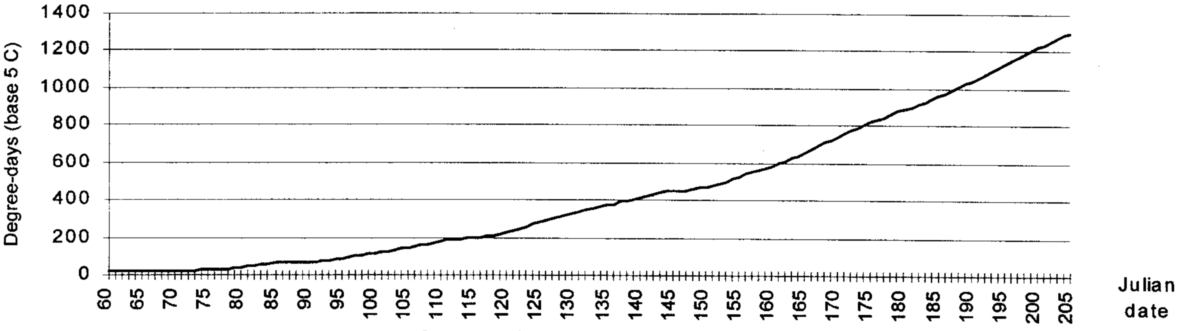
Figure 1. **Growth of *L. decidua* seed cones at Hemeiusi-Bacau, Romania, 1991-1995.**

RESULTS AND DISCUSSION

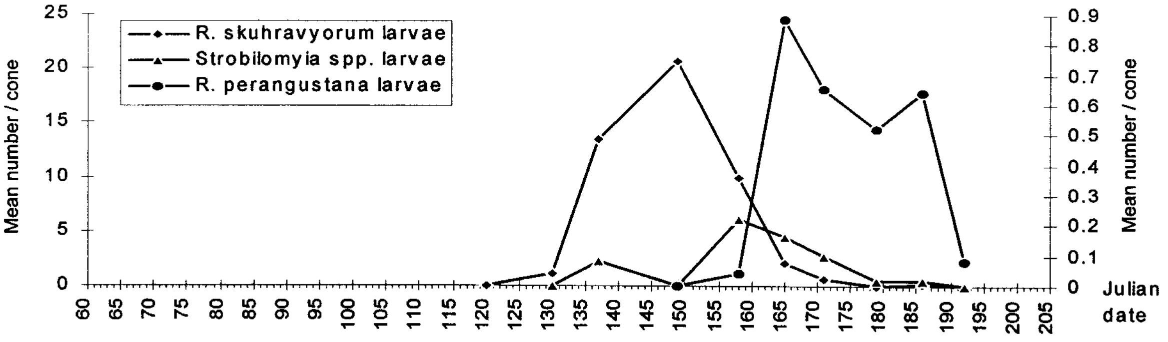
Growth and development of *L. decidua* cones. The increase in cone length and diameter began each year within the third or even the second decade of March (e.g., 1994, 1995). Important differences between years were observed (Fig. 1), likely due to diverging trends in weather patterns between January and March (Table 1). During this study, 1991 and 1992 were the coolest years, and 1994 and 1995 the warmest. In 1993, an exceptional year, January was warm (mean=0°C; 36.4°d accumulated), but March was the coldest of the five years with mean daily temperature



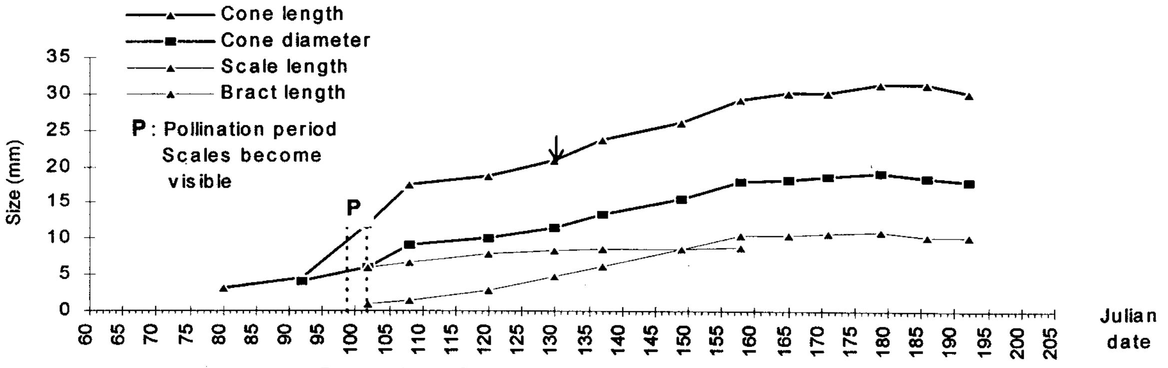
Dynamics of temperature and rainfall



Accumulation of degree-days



Dynamics of insect population density inside the cones
(Left scale for R. skuhravyorum; right one for the other species)



Dynamics of cone growth and development

Figure 2. Relationships between *L. decidua* seed cone development and cone colonization by insects, 1991.

below 0°C for 14 days and minima as low as -15.4°C.

In 1991, the buds of seed cones began swelling between 21-30 March (JD 80-90) and bud burst occurred within the first two days of April (JD 91-92) (Fig. 2). Typically, bud burst occurred after about 14 d with mean daily temperatures higher than 5°C and required about 74°d. Pollination occurred between 08-11 April (JD 98-101) and required 106-120°d. Ovuliferous scales appeared on 10 May (JD 130), when bracts ceased to grow and scale length was more than 50% of the bract length, and when the temperature sum was 324°d. Cone growth (i.e.,

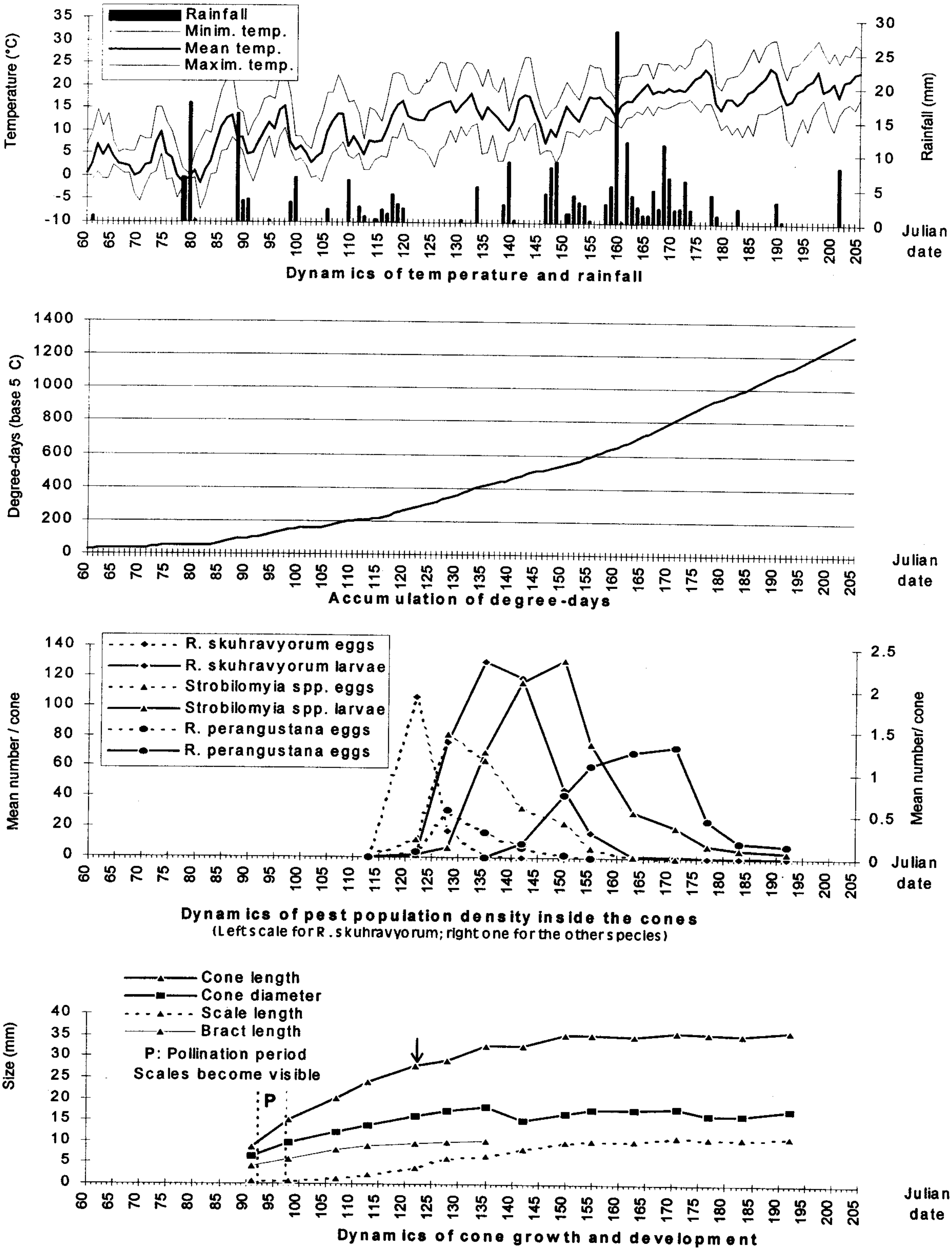


Figure 3. Relationships between *L. decidua* seed cone development and cone colonization by insects, 1992.

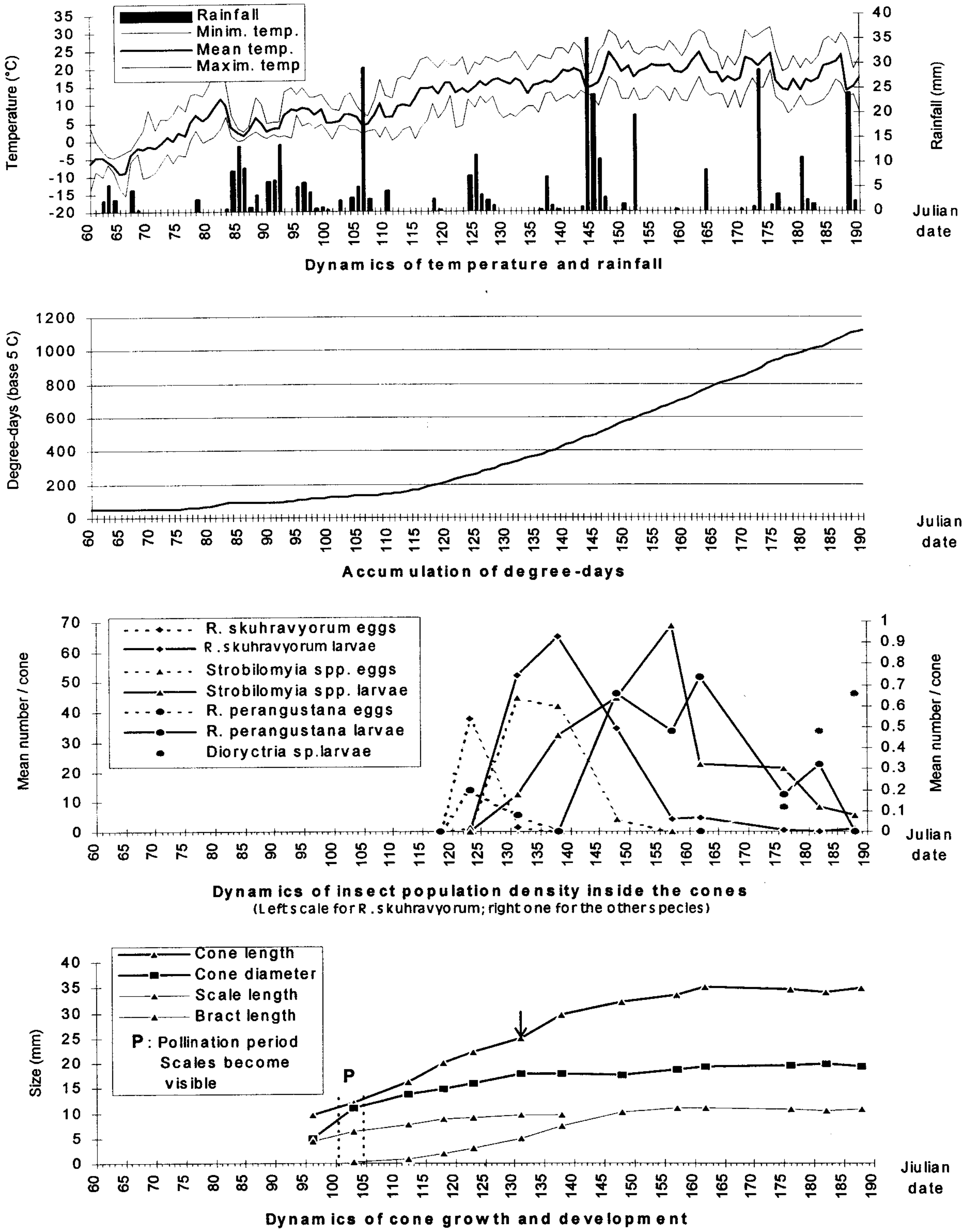


Figure 4. Relationships between *L. decidua* seed cone development and cone colonization by insects, 1993.

changes in length and diameter) stopped around 07-14 June (JD 158-165), when the temperature accumulation was 559-652°d.

When first sampled on 31 March 1992 (JD 91), seed cone buds had already burst open and had already reached 25% of their final length (Fig. 3). This suggested that bud burst had occurred around 25 March (JD 85), when the weather had improved after a period with mean daily temperatures of about 0°C or lower. The shedding of pollen which had not

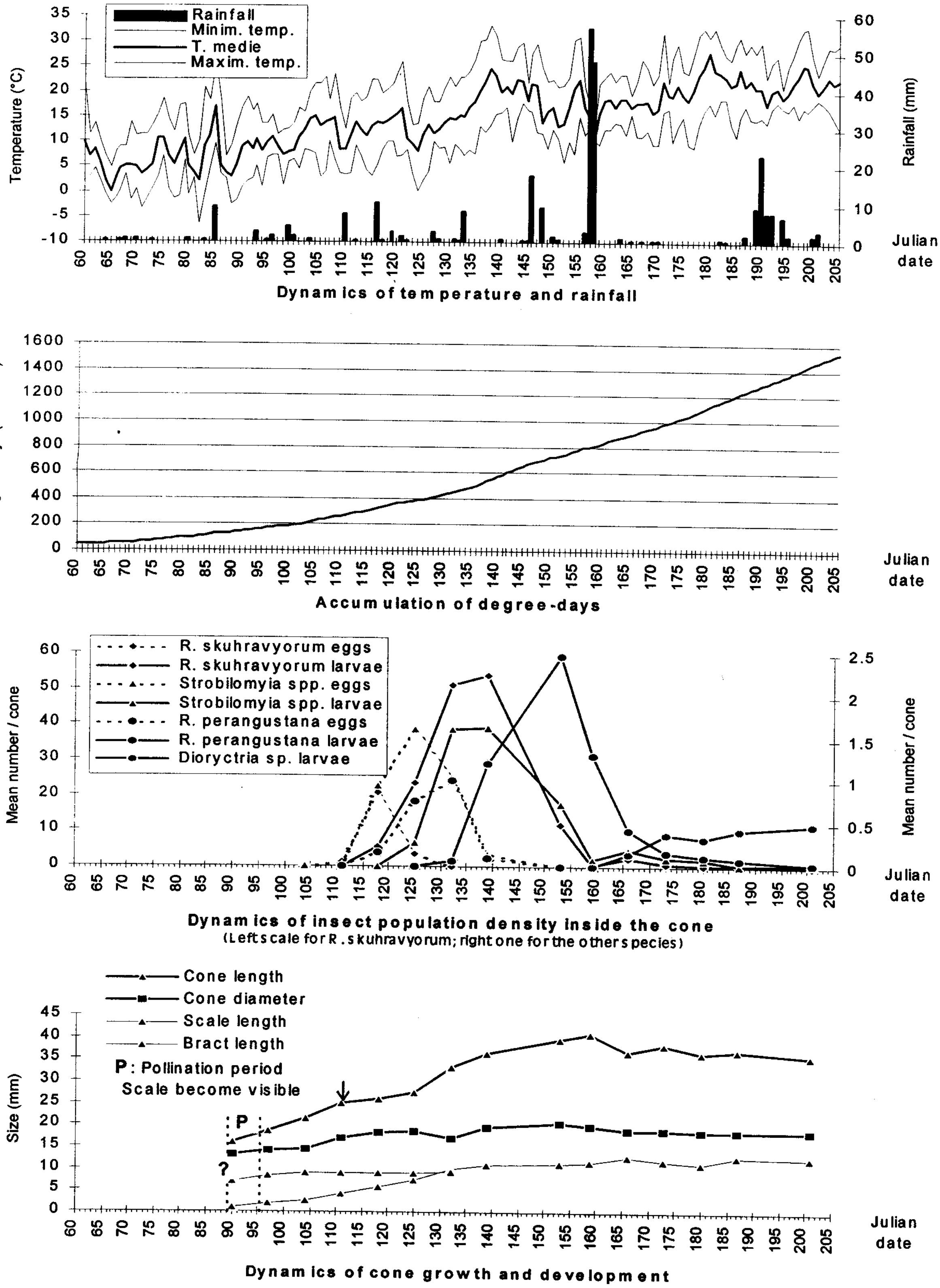


Figure 5. Relationships between *L. decidua* seed cone development and cone colonization by insects, 1994.

begun on 31 March, was completed on 07 April (JD 98), suggesting that pollination had occurred between 01-06 April and had required 102-144°d. Ovuliferous scales appeared between bracts on 01 May (JD 122; 281°d), and cone growth was completed around 03 June (JD 155; 590°d).

In 1993, the situation was similar (Fig. 4). When first sampled on 06 April (JD 96), seed cones had already reached about 29% of their final length. Bud burst probably had occurred between 26-31 March (JD

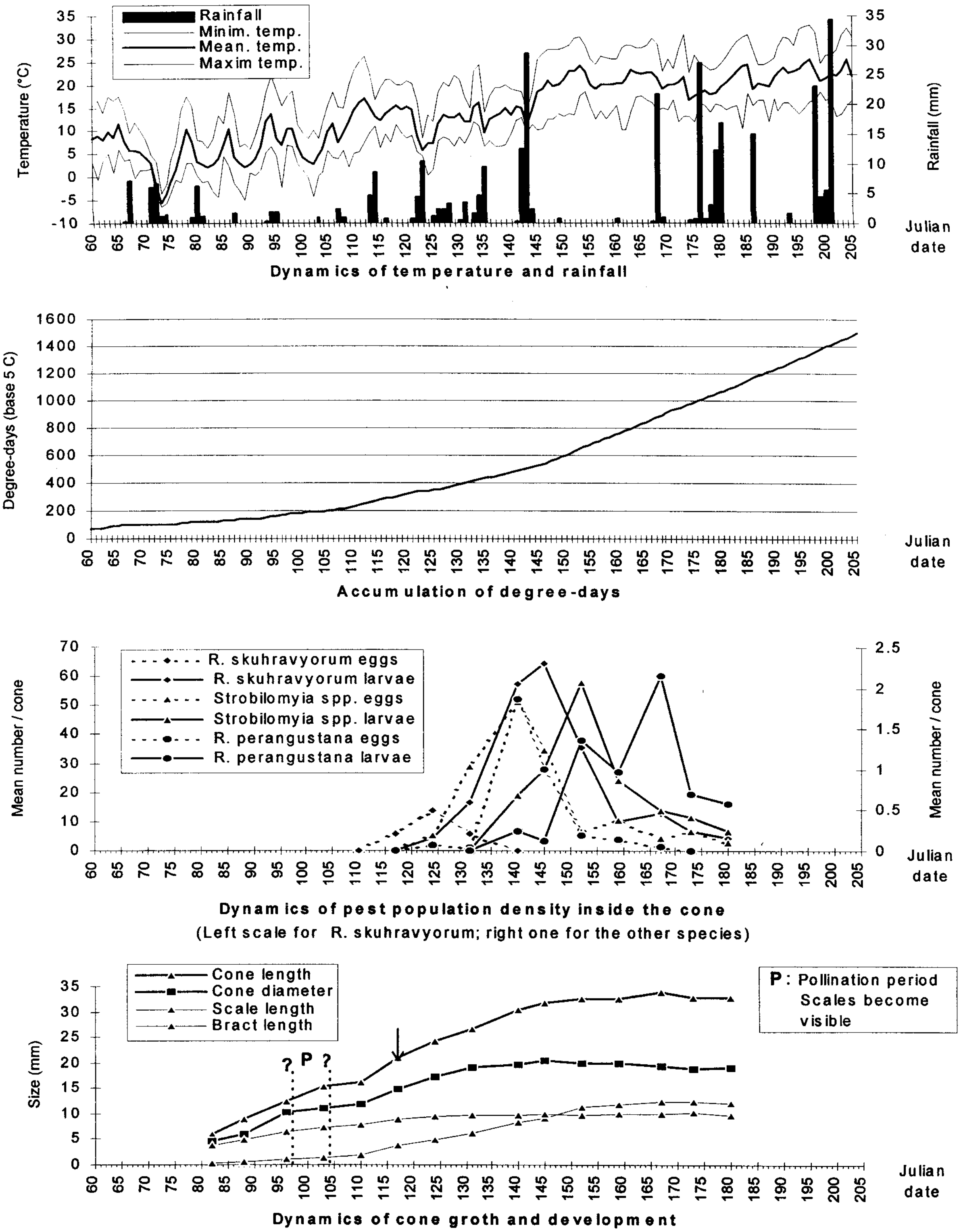


Figure 6. Relationships between *L. decidua* seed cone development and cone colonization by insects, 1995.

86-90), when the temperature sums were 82-92°d. Pollination took place between 10-14 April (JD 100-104), requiring 121-130°d. On 11 May, ovuliferous scales were visible among the bracts, suggesting scales had appeared during the period of 03-11 May, and had required 245-328°d. Cone length increased until 11 June (JD 162), but the length of ovuliferous scales ceased to increase on 06 June (JD 157). Thus, I assumed that cone growth was completed on 06 June (669 DD). Subsequent increases in cone length and

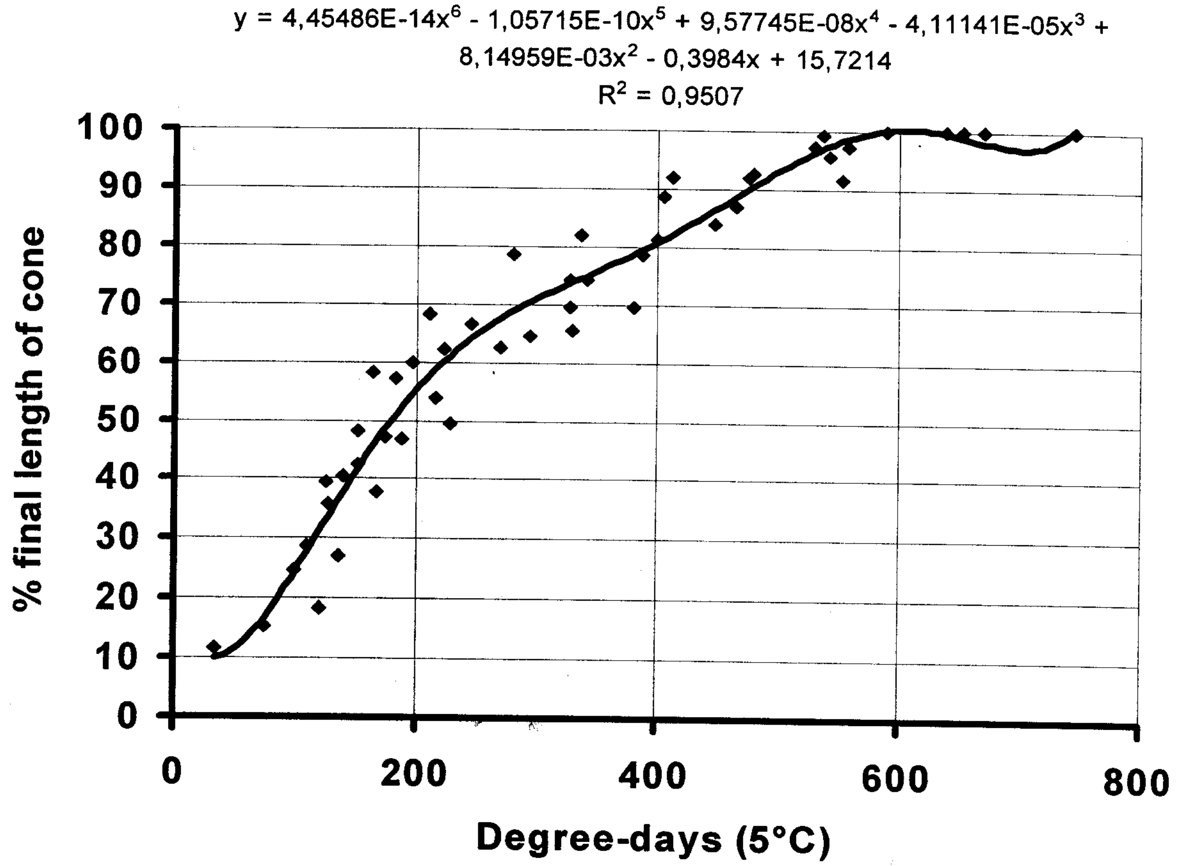


Figure 7. Estimates of degree-day requirements for the development of seed cones obtained at Hemeiusi-Bacau, Romania.

diameter were attributed to sampling errors.

The 1994 estimates of degree-day requirements for the main phenological phases of cone development were similar to those obtained in 1993 (Fig. 5), although bud burst occurred much earlier. In 1995, cone growth and development followed a similar trend (Fig. 6), except that a late frost killed almost all cones shortly after bud burst, between 13-18 March (JD 72-77). Only cones that were less developed and probably more resistant survived.

The increase in cone length was faster during the first part of the growing phase than in the second one. The polynomial relationships between cone length and temperatures revealed three inflection points, which marked obvious changes in the curve's slope (Fig. 7). The first inflection occurred when temperature sums reached 65°d or 15% of the final cone length. The second deviation happened after 250°d had accumulated or when the cone had attained 65% of its final length. The last inflection occurred at 590-600°d when the cone had reached its final length. These points divide the curve in four segments, each corresponding to a phase of cone growth and development (Fig. 8).

The first phase, referred to as seed cone expansion, was characterized by an increase in the size of the bud and lasted until bud burst occurred, typically requiring 65-75°d.

The second phase was typified by a rapid growth of the cones. Only bracts which grew rapidly were visible during this phase. Meanwhile, ovuliferous scale growth was slow, especially before pollination which took place when temperature sums were between 110-160°d. Our estimates of degree-day requirements for the appearance of ovuliferous scales was about 250°d. At that time, bract growth was almost completed. Thus, this phase corresponded predominantly to a period of bract growth (Roques 1983, 1988a, b; Yao *et al.* 1991) or bract stage (Roques *et al.* 1995).

The third phase was a period of slow cone growth referred to as the ovuliferous scale growth phase (Roques 1983, 1988a, b; Yao *et al.* 1991; Turgeon & de Groot 1992). This phase was characterized by the continuous scale growth and the gradual "disappearance" of the bracts between the scales. It ended when cone length and diameter stopped increasing. During the first part of this phase, bracts were still longer than ovuliferous scales. This period, referred to as the bract-scale stage (Roques *et al.* 1995), required about 360°d. Scales became as long as bracts when temperature sums were about 500°d. At that moment, the scale-bract stage ended and the scale stage (Roques *et al.* 1995), which continued during the fourth phase of cone development, began.

The last phase was the period of cone lignification and seed maturation. During this phase, cones did not grow, but gradually turned brown.

Estimates of degree-day requirements for the different phenological phases of *L. decidua* cone development were lower than those of *Picea mariana* (Mill.) B. S. P. (Pinaceae) (Prévost 1986). This observation is consistent with the fact that *L. decidua* is a subalpine species adapted to cold climate and to short period of development whereas *P. mariana* grows naturally at high and low altitudes under a wide range of climatic conditions and where the growing season can last up to 160 d (Farjon 1990). Because of its short growing season, *L. decidua* seed cone bud burst must occur early in the season. Such early development also means that late frosts often destroy a significant portion of the cone crop at both high (Roques 1988a, b; Shearer 1990) and low altitudes. Often the minimum daily temperatures were not low enough to kill seed cones, but could nonetheless negatively influence pollen cone development (Barner & Christiansen 1960; Christiansen 1960). This could explain the high proportion of empty seeds observed in cones of *L. decidua* (Kosinski 1982, 1987).

Colonization of *L. decidua* cones by insects The most destructive insects of *L. decidua* cones and seeds at the Hemeiusi-Bacau orchard were *Resseliella skuhravyorum*, *Strobilomyia* spp. - predominantly *S. melania* and *S. infrequens*, and less frequently *S. laricicola* – and *Retinia perangustana. Dioryctria abietella* was responsible for destroying a high percentage of cones (Olenici 1990, 1991, 1998).

The development of insects was strongly influenced by weather conditions. Some insects colonized cones at the time, or shortly before, ovuliferous scales appeared, between the end of the second phase and the beginning of the third phase of cone development.

The first eggs of *R. skuhravyorum*, *S. laricicola* and *R. perangustana* were found at the same time except in 1991 when only larvae of these species were found and in 1995, when those of *R. skuhravyorum* were detected first. Fluctuations over time in densities of these species within cones however differed among species (Figs. 2-6). Eggs of *R. skuhravyorum* were found within the cones for about three weeks and the maximum number of eggs per cone was generally recorded immediately after the beginning of the oviposition period, as was seen in 1992.

Typically, the first larvae were found within a week of the beginning of oviposition suggesting that under field conditions the embryonal development lasted at most seven days. The maximum number of larvae per cone was obtained about 15-20 d after the beginning of egg-hatch. The last eggs within the cones were found also at about the same time. Shortly after that, larvae began to leave cones that were at the end of scale-bract stage or at the beginning of the scale stage indicating that larval development in the cone was completed in about three weeks. Two weeks after the beginning of the scale stage, 80-90% of the larvae had exited the cones.

Typically, the estimates of degree-day requirements for the beginning of *R. skuhravyorum* oviposition and egg- hatch were about 229-245°d and 294-330°d, respectively. This indicates that requirements for embryonic development were about 50°d. The last eggs within the cones were found when temperature sums were about 413-447°d. The first larvae left the cones when sums had reached 537-552°d. Thus estimates for larval development were about 255°d. The maximum number of larvae per cone was recorded after 447-529°d had accumulated. By the time temperature sums had reached about 770°d, more than 90% of the larvae had dropped into the litter.

The species of *Strobilomyia* infested the cones in the same order as has been previously reported (Roques 1983, 1988a, b, 1989; Roques *et al.* 1984). *Strobilomyia laricicola* was the first species to oviposit and was followed by *S. melania* and *S. infrequens.*

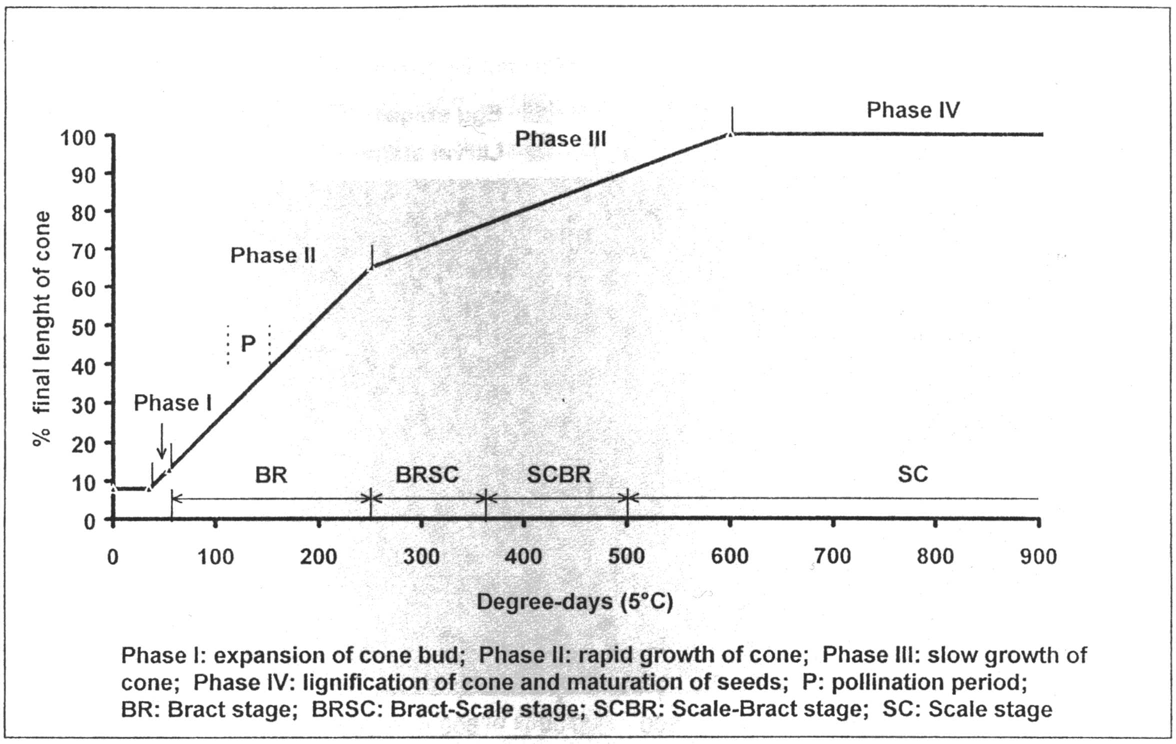


Figure 8. Model of growth and development of *L. decidua* seed cones in relation to temperature sums at Hemeiusi-Bacau, Romania.

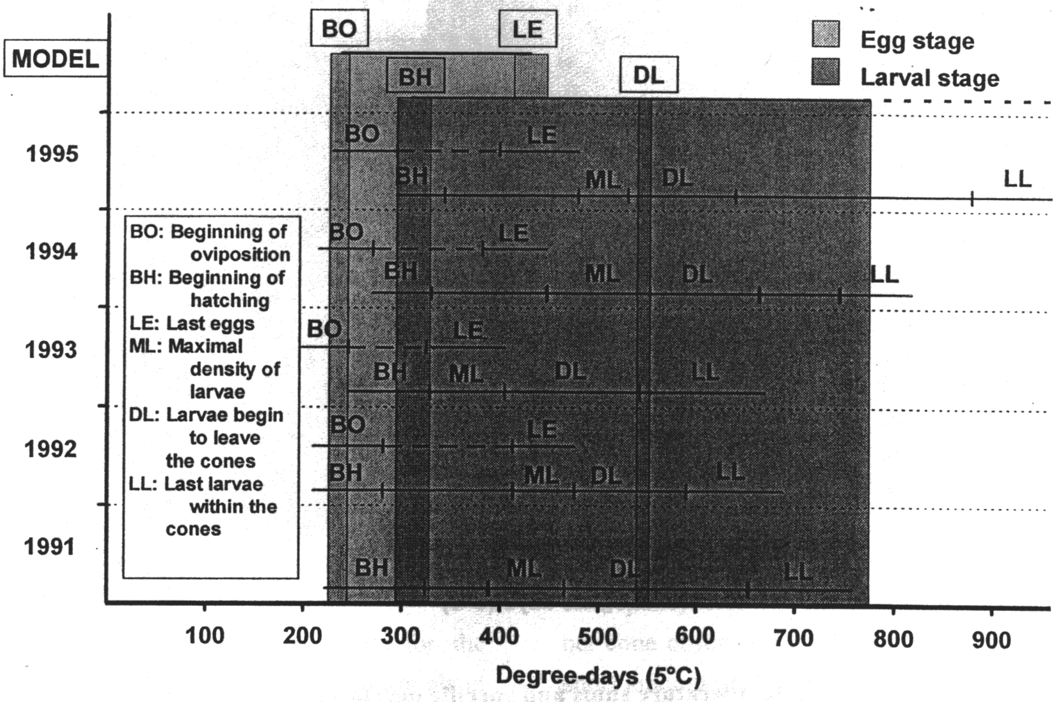


Figure 9. Relationship between temperature sums and specific developmental stages of *Resseliella skuhravyorum* at Hemeiusi-Bacau, Romania.

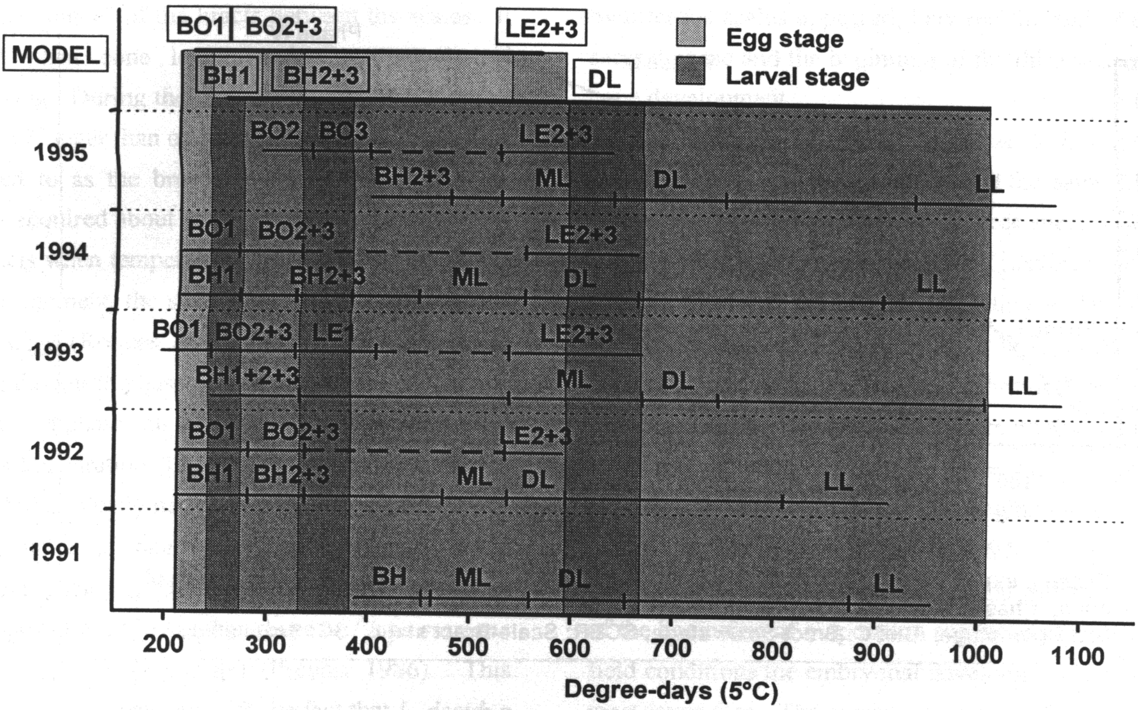


Figure 10. **Relationship between temperature sums and specific developmental stages of three species of *Strobilomyia* at Hemeiusi-Bacau, Romania. Legend as in Fig. 9, 1: *S. laricicola*, 2: *S. melania*, 3: *S. infrequens*.**

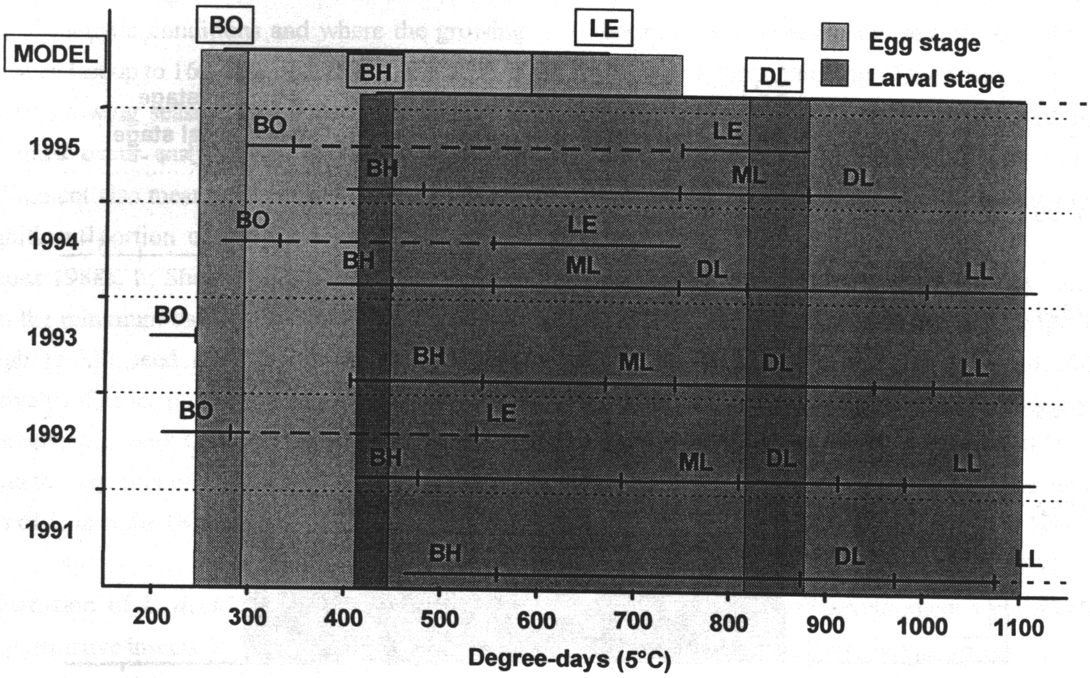


Figure 11. **Relationship between temperature sums and specific developmental stages of *Retinia perangustana* at Hemeiusi-Bacau, Romania. Legend as in Fig. 9.**

However, all three species began oviposition within a week of each other. The first eggs of *S. melania* and *S. infrequens* were found practically at the same time. The first eggs of *S. laricicola* were found between the end of the second phase and beginning of the third phase of cone development, not at the time of pollination as was previously reported by Roques (1983, 1988b) and Roques *et al.* (1984). Few eggs of *S. laricicola* were found, and usually they were present in cones for only 1-2 weeks, indicating that this species was rare in the orchard. This conclusion is consistent with the very low percentages (*ca.* 10%) of cones damaged by this species in the orchard, and is also consistent with observations made by Roques (1983, 1989) and Roques *et al.* (1984), indicating that this species was predominant mainly at high altitudes.

The maximum number of *Strobilomyia* spp. eggs was recorded 1-2 weeks after the beginning of oviposition. The last apparently viable eggs were found five weeks after the beginning of oviposition (Figs. 2-6). Generally, the first larvae appeared in cones about a week after the beginning of oviposition. In 1992 and 1994, the first eggs and eggshells of *S. laricicola* were found at the same time, whereas in 1994 and 1995, the first larvae of *S. melania* were recorded only two weeks after the first eggs of *Strobilomyia* spp. had been found. The maximum number of larvae per cone was observed on the third week following the beginning of egg-hatch. After that, larvae began to leave cones. As a result, the development of second and third instars lasted about 21 d. Roques *et al.* (1984) reported much longer duration of larval development for these species at 1200 m, although similar durations have been reported for other species of *Strobilomyia* that infest cones of *Larix laricina* (Du Roi) K. Koch (Amirault & Brown 1986; Amirault 1989; McClure *et al.* 1996) or *Picea mariana* (Sweeney & Turgeon 1994).

Estimates of degree-day requirements for the beginning of the oviposition by *S. laricicola* was about 197-281°d, but more likely 210-245°d (Fig. 10). The first hatched eggs were found when temperature sums were between 210-281°d, suggesting that egg-hatch probably began between 245-270°d and that requirements for embryonic and first instar development was only 30°d. Oviposition by *S. melania* and *S. infrequens* usually began when temperature sums were between 245-338°d. In 1995, the beginning of *S. melania* and *S. infrequens* oviposition occurred when about 294-343°d and 343-400°d, had accumulated. This difference in development between these two species was more conspicuous than with the other species. In addition, *S. laricicola* was practically absent from the cones in that year. This is probably due to the very low temperatures recorded after bud burst of *L. decidua* that damaged seed cones and the species of herbaceous flowers used by adult flies to feed. Thus, the most probable estimates for the beginning of oviposition and egg-hatch by these species were 294-328°d and 328-382°d, respectively. It means that, the requirements for the embryonic and first instar development were about 45°d. The last viable eggs and the maximum number of larvae per cone occurred when heat sums were at 542-590°d. Larvae began to leave cones after 590-669°d had accumulated. Thus, requirements for the combined development of second and third instars were estimated at about 275°d. Some larvae could still be found in cones after 1000°d had accumulated.

Retinia perangustana began oviposition as early as the onset of the third phase of cone development (Figs. 3-6) and continued until the end of that phase. These results differ from previous reports indicating that oviposition by *R. perangustana* was beginning at a later phase of cone development (Roques 1983; Olenici 1990). This is because these authors failed to examine the bud scales of the cones, where most of the eggs of *R. perangustana* and a high percentage of eggs of *R. skuhravyorum* are laid. On the other hand, I have noted that eggs of *R. perangustana* were also laid in pollen cones, between the bud scales and the pollen cone. Larvae hatching from these oviposition sites later crawled towards seed cones, thus explaining the discrepancy between the number of eggs and larvae per cone observed in 1992 and 1993, as well as the short amount of time eggs are present in cones (e.g., 1993). Our observations on the dynamics of the number of eggs per cone were also consistent with the dynamics of the number of adults caught in pheromone traps (Olenici *et al.* 1995). The overlap between the date the first adults were trapped and the date the first eggs were found in the cones indicates that oviposition began soon after adult emergence (Olenici 1994). Generally, the flight and the oviposition period lasted four weeks, although in 1995 it lasted six weeks. Theearliest larvae were found about two weeks after oviposition had begun and the last eggs hatched at the end of the third/beginning of the fourth phase of cone development. This was also the time when the maximum number of larvae per cone was recorded.

Estimates for the earliest and latest beginning of oviposition were 197-245°d in 1993 and 294-343°d in 1995, respectively (Fig. 11). Thus, requirements for the beginning of oviposition likely are 245-294°d. Similarly, the earliest and latest hatching occurred when temperature sums were 381-447°d in 1994 and 412-476°d in 1992. The mean interval for hatching could be around 412-447°d. Consequently, requirements for the embryonal development would be about 160°d. This estimate is consistent with previously published calculations by Olenici (1994), which had reported that larvae took 8-10 d to hatch at 18-22°C. Field observations also revealed that the last eggs were found in cones when temperature sums were between 590-745°d. These observations suggest that flight and oviposition were not only influenced by temperature, but also by wind and rainfall. This rather long period of oviposition influenced the duration of the period when the maximum number of larvae occurred. Degree-day requirements for larval development were estimated at about 415°d because the most probable interval for leaving the cones was when heat sums were 816-878°d. More than 90% of the larvae left the cones before 1100°d had accumulated.

In 1993 and 1994, cones were also damaged by larvae of *Dioryctria abietella.* The first larvae appeared 1-2 weeks after cone growth had stopped (Figs. 4-5), when temperature sums were 816-905°d. There was a drastic increase in the number of larvae per cone between 25 June (JD 176; 949°d) and 07 July (JD 188; 1100°d) 1993, but not as pronounced in 1994.

CONCLUSIONS

Development and growth of *Larix decidua* seed cones consisted of four phases that could be distinguished morphologically and that occurred at specific degree-day requirements. The requirements for the first phase, seed cone bud swelling, were between 35 and 65-75°d. The second and third phase, characterized by rapid and slow growth rate, respectively, ended when temperature sums were about 250°d and 600°d, respectively. At that time, the fourth phase, identified as the period of cone lignification and seed maturation, began.

Bract elongation occurred during the second phase of cone development, the bract stage. There was considerable overlap between the bract-scale stage which required about 250-365°d, and the scale-bract stage which required about 365-500°d and occured in the third phase. The scale stage overlapped with the remainder of the third phase and the fourth phase.

The succession of the main pest insects that damaged the cones and seeds of *L. decidua* at Hemeiusi-Bacau was as follows: *Resseliella skuhravyorum*, *Strobilomyia laricicola*, *S. melania*, *S. infrequens* and *Retinia perangustana* with occasional occurrences of *Dioryctria abietella.* All these species, except for *D. abietella*, initiated cone colonization at the end of the second phase and the beginning of the third phase of cone growth, and developed either exclusively during the third phase (e.g., *R. skuhravyorum* and *Strobilomyia* spp.) or during the third and part of the fourth phase (e.g., *R. perangustana*). *D. abietella* could be found within the cones only during the fourth phase.

Estimates of degree-days requirements obtained with a threshold value of 5°C starting on 01 January for egg colonization were 229-245°d for *R. skuhravyorum*, 210-245°d for *S. laricicola*, 294-328°d for *S. melania* and *S. infrequens*, and 245-294°d for *R. perangustana.* Those for the beginning of hatching were 294-330°d for *R. skuhravyorum*, 245-270°d for *S. laricicola*, 328-382°d for *S. melania* and *S. infrequens*, 412-447°d for *R. perangustana* and 816-905°d for *D. abietella.* The last apparently viable eggs were found when temperature sums were about 413-447°d for *R. skuhravyorum*, 542-590°d for *S. melania* and *S. infrequens*, 590-745°d for *R. perangustana.* Estimates for the beginning of larval exit were 537-552°d for *R. skuhravyorum*, 590-669°d for *S. melania* and *S. infrequens* and 816-878°d for *R. perangustana.* More than 90% of the larvae *R. skuhravyorum*, *Strobilomyia* spp. and *R. perangustana* had left the cones when about 770°d, 1000°d and 1100°d had accumulated, respectively.

The maximum number of larvae per cone was recorded at the same time as the last eggs were found, or between that moment and the one at which larvae began exiting cones.

Estimates of degree-day requirements for the development of the embryo, and of the first instar in the case of *Strobilomyia* spp., were 50°d for *R. skuhravyorum*, about 30°d for *S. laricicola*, 45°d for *S. melania and S. infrequens*, and 160°d for *R. perangustana*. Estimates for larval development were 255°d for *R. skuhravyorum*, 275°d for *S. melania* and *S. infrequens* and 415°d for *R. perangustana*.

ACKNOWLEDGEMENTS

This study was conducted at the Experiment Station for Spruce Culture, Campulung Moldovenesc, Romania and at the Institute of Landscape Planning and Management (Institut für Landespflege) at Freiburg, Germany, where I stayed from 1 December 1995 to 31 August 1996 thanks to a scholarship from the European Union in the JEP-07975-95 TEMPUS project. I am deeply indebted to all those who have made this work possible, as well as to my colleague G Maciuca, from the English Department, who did her best to put my message across.

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