A HEAT SUM MODEL FOR LOBLOLLY PINE POLLEN DEVELOPMENT

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Abstract. Catkin development was recorded at 2 to 7-day intervals in February and March of 1988 to 1992 for 90 ramets from 31 families at the Weyerhaeuser Company's loblolly pine seed orchard in Lyons, Georgia. Four to twelve clusters per ramet were observed each year and scored for development on a 6-point scale. The timing of catkin development varied widely over the study period. For example, the date when pollen release began (score = 4.0) varied from February 17 in 1990 to March 6 in 1988 for the earliest family and from March 7 in 1990 to March 26 in 1988 for the latest family. A heat sum model was developed to account for this annual variation using the first four years of data from 12 families measured all five years. The model which explained the most variation accumulated heat units above a threshold of 37 °F starting January 17. Different families required different heat sums to reach a given stage of catkin development. The model was validated using development data from 1992. The model predicted the time of 50 % pollen shedding (score = 5.5) within 1 day for 7 families, within 2 days for 3 more families, and within 4 and 6 days for the remaining two families.

Keywords: Loblolly pine, seed orchard, clonal, pollen, degree hour, heat sum, model.

INTRODUCTION

The phenology of pine pollen development is known to vary among years, among species, and among individuals within a species (Dorman and Barber, 1956; Blush, et aL, 1993, and many others). In Loblolly pine seed orchards, between family variation of pollen shedding has been reported by Brarnlett and Bridgwater (1989). The timing of clonal pollen release is useful to orchard managers for the scheduling of operations related to pollen collection, and the estimation of interclone crossing potentials and genetic composition of the seed crop. Wheeler and others (1993) believe that phenology is the most important influence on gene flow in forest seed orchards.

Clones tend to maintain their relative rank in timing from year to year (Blush, et al., 1993), and experienced workers can predict pollen release by monitoring catkin development and noting the relative timing of shedding of different clones for several years. However, the development of a heat sum model to predict different stages of pollen development could be useful for: 1) making predictions earlier in the season, 2) allowing for continuous adjustments to predictions based on updates in weather data, 3) quantifying clonal composition of the pollen cloud at any given time, and 4) reducing the expertise needed to make predictions. Such a model would not replace the need for field observations, but could reduce the work required by determining when field observations should begin.

A heat sum model predicts that a certain developmental event will occur when a defined heat unit total is reached. Heat units are accumulated during days or hours of the growing season during which the temperature is above a defined threshold value. The parameters of the model are: I) the **start date** of the growing season, 2) the **threshold** temperature, and 3) the **critical heat sum** required for the target event to occur. Many assumptions and simplifications are made; the limitations of heat sum models have been well reviewed by Wang (1960). Nevertheless, they have had useful applications in agriculture (Wang, 1960) and

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forestry, including the description of bud development in Douglas-fir (Thomson and Moncrief 1982), red pine (Sucof 1971) and Loblolly pine (Boyer, 1970), and pollen shedding in southern pine (Boyer, 1978).

The objective of this study was to create a heat sum model that would account for the annual variation in timing of pollen development for different clones of Loblolly pine. The model would use a single threshold temperature and start date for all clones in the orchard, but each clone would have a different critical heat sum. The model would be used to predict the timing of pollen shedding based on weather data in future years.

METHODS

Pollen Development Classification System

A method for consistent assessment of catkin development and degree of pollen shedding was a prerequisite to model development. Bramlett and Bridgwater (1989) presented a Pollen Development Classification System (PDCS) that measured development on a six-point scale; pollen shedding begins at a score of 4.0 and becomes measurable at 5.0 (Table 1). An important feature of this scale is that in addition to identifying the stage of pollen release, the percentage of pollen shed is estimated.

TABLE 1. Pollen Development Classification System. (Abbreviated from Bramlett & Bridgwater, 1989).

PDCS stage	Description	Approximate date for Lyons, GA
1.0 -3.9	Various stages of catkin elongation.	Fall - Feb.
4.0	Pollen release begins, less than 10% of pollen released.	mid Feb. - Mar.
5.0	Pollen release increases, more than 10% released.	Mar.
5.2	20% released.	
5.5	50% released.	
5.9	90% released.	
6.0	All pollen released.	Apr.

These stages apply to individual catkins. When assigning a PDCS score to a cluster comprised of catkins in various developmental stages, the cluster was scored to reflect the average of the catkins.

Field measurements of pollen development

Observations of catkin development were made on 90 ramets from 31 families from 1988 to 1992 at the Weyerhaueser Company seed orchard in Lyons, Georgia. The families included in the study varied from year to year due to 1) roguing in the orchard, 2) reducing the overall sample size, and 3) missing the shedding season of early clones in 1989. Seven families were measured all five years and twelve were measured in all but 1989. The model described in this report is based on those 12 families. Ten to twelve clusters distributed throughout the crown of each ramet' were tagged and scored at two to seven-day intervals during the flowering season. Ramet scores were means of ramet clusters, weighted by the number of catkins in the clusters. Based on 1988 preliminary results, the number of families and the number of ramets per family were reduced, and scores of ramets of the same clone were averaged when clones were represented by more than one ramet.

Temperature data was recorded at hourly intervals by an onsite weather station. Missing observations were filled with data from the nearest National Weather Service stations.

In 1989 only 4 clusters were measured and the beginning of shedding season was missed.

Choosing the heat sum model parameters

The first step was to choose the target developmental stage. We examined targets of 4.0, 5.0 and 5.5; the target used for example in this report is a PDCS stage of 5.5, the stage when half of a clone's pollen is shed. This date was determined for each clone by graphical analysis of the plot of average PDCS score over time. The heat sum at which stage 5.5 was reached depends on the threshold and start date. These two parameters of a heat sum model are correlated with each other, complicating the task of choosing best fit values (Boyer, 1973). The method used is an adaptation of Boyer's work with Longleaf pine. He modeled the timing of pollen shedding of a *single population,* choosing the start date and threshold that reduced the variation over years of the critical heat sum: the heat sum accumulated at the time of pollen shedding. Once these two parameters were determined, the critical heatsum required in a given year was related to and modified by the length of time required to reach that heat sum. In our study, we proceeded similarly for *each family,* choosing a different start date and threshold for each family. We then chose single values for these two parameters that were the best overall choice for *all* families. The model critical heat sum was calculated for each family as the average observed critical heatsum over years.

To determine the best start date and threshold for a single family, heat sums were calculated *using* all combinations of values of 30 to 60 degrees F. for the threshold and Julian day 1 to 42 (Jan 1 to Feb 11) for the start date. For each combination, the heat sum at which each clone reached a score of 5.5 was determined for each year. The standard deviation and coefficient of variation of these heat sums over years were determined for each combination. The best combination, **i.e.** the model that explained the most variation, was determined by examination of the effect of start date and threshold on standard deviation and coefficient of variation. This analysis is confounded because when the threshold is lowered, standard deviation will *increase* due to the size of the means while coefficient of variation will *decrease* because annual variation *is* dampened (Boyer, 1973). However, minima and slopes of these functions indicated the best threshold and start date parameter values.

Model Validation

The model predicts that PDCS stage 5.5 is reached when the heat sum reaches a certain value for a given clone. The model's accuracy can be checked by comparing the day that this was observed to occur to the day predicted to occur for each year. This was done for the years used in model formation, 1988 to 1991, and for 1992, a year of data independent from the model formation data.

RESULTS AND DISCUSSION

The variation in timing of all (31) clones in a single year (1988) was described by Branilett and Bridgwater (1989). Their plot also showed the similarity in shape of the development curves for the different clones. For this study, plots of PDCS score against time for all years were made for each clone. Figure la is an example plot for a single clone, "19", and shows patterns that are typical of all the clones: 1) ramets of the same clone in a given year develop synchronously, 2) large differences exist in the timing of pollen development between years of a given clone. For this clone, there was a 4 or 5-day difference between the times the earliest and latest ramets reached stage 5.5 in a single year while there were over 20 days difference between the earliest and the latest year. These results gave us the confidence to average scores from ramets of the same clone for a given year. Note that in a plot of these averages (figure lb), the development curves for 1990 and 1988 fluctuate. This is because data were averaged by date and ramets were not all measured on the same day.

Plots of the average development score for a family allowed determination of the dates that PDCS stage 5.5 (or other stage) was reached in the various years by the family. In figure lb, the vertical arrows placed at the intersection of the curves and the target PDCS stage of 5.5 intersect the horizontal axis at these dates. Some adjustment is required to accommodate fluctuating lines, but we considered that this error was not important in estimating dates to the nearest day. Table 2 shows the Julian dates at which the 12 clones used in the model attained PDCS scores of 4.0 and 5.5. Field measurements began late in 1989 and some clones had already finished shedding pollen before they were visited. The results in Table 2 show that the relative timing of clones remains stable over time, but the magnitude of the differences in timing and the amount of overlap *of* sheddin^{g} is variable. The difference between when the earliest and latest clone reached stage 5.5 was 16 - 18 days for most years and there was no overlap in shedding (score 4.0 - 6.0) between the earliest and latest clones. In 1992, however, the difference is only four days, so most of the clones were shedding at the same time. This phenomenon may be explained by the high temperatures proceeding and during pollen

FIGURE 1. Pollen Development Classification Scores for Loblolly pine clone "19" plotted over day. Weyerhaueser company seed orchard, Lyons, GA, 1988 - 1991.

a) PDCS scores for individual ramets; three for 1990, one each for 1989 and 1991, and eight for 1988.

b) Date that average PDCS score (means of all ramets measured in a given year) reached 5.5, 50% of pollen shed, in 1988 - 1991. Fluctuating average in 1990 and 1988 occurs because different ramets were measured on different days.

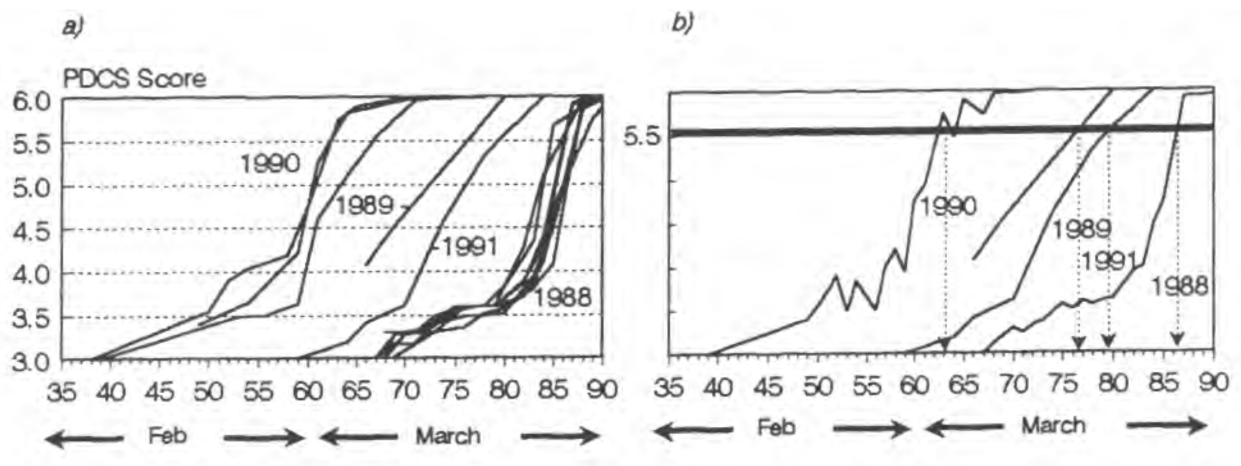
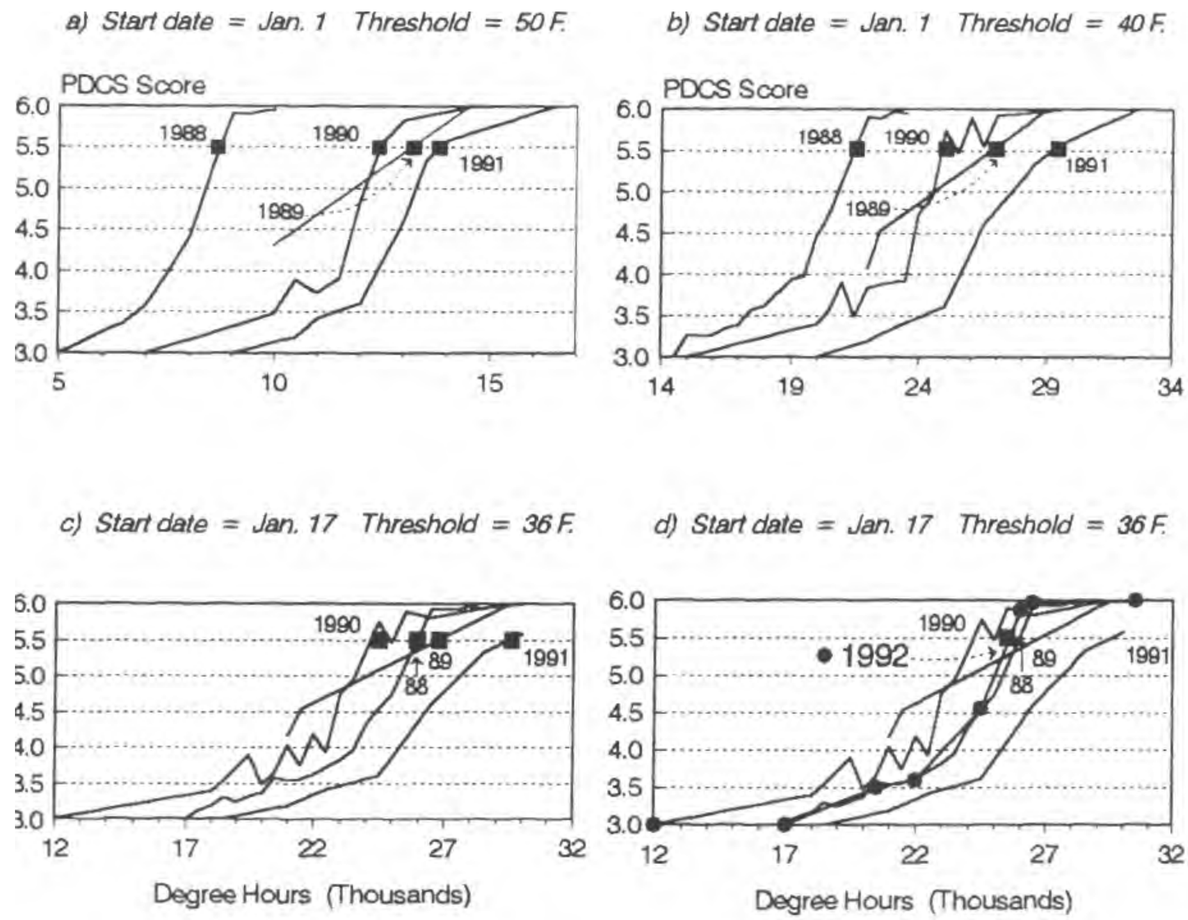


TABLE 2. Dates that PDCS score reached stages 4 and 5.5 in 1988 - 1992. Clones are ordered based on average development dates.

CLONE	*1988*		*1989*		*1990*		*1991*		*1992*	
	4	*5.5*	*4*	*5.5*	*4*	*5.5*	*4*	*5.5*	*4*	*5.5*
53	66	70	-	-	48	54	59	64	64	67
22	72	78	-	-	-	-	61	66	60	65
43	76	83	-	-	44	52	64	72	65	68
28	76	83	-	-	44	55	66	72	65	68
00	76	81	56	65	51	57	67	73	65	68
33	75	81	62	71	54	60	67	73	66	68
39	81	85	66	74	57	63	71	75	66	69
20	81	86	61	74	59	65	70	75	66	68
19	83	86	65	76	58	63	71	79	66	70
37	84	87	60	75	51	64	71	79	67	70
73	83	87	-	-	60	64	72	77	68	70
31	85	88	71	78	65	70	77	82	68	71

FIGURE 2. Effect of start date and temperature threshold on the heat sum development curve of Loblolly pine clone 19 in years 1988 - 1991. Year 1992 is included in *d).*



111^ 1 0!• 51 q17^ 110R1 071 710:1• 7i;1 vi^l'l071 371 1 O0 1B01 0711 0•
11377211071 0t' 11031 511•71 7 0 11117 1 . 07 1,01110113i p17 10712 19 10 5•5111 '0375 1988 1991•
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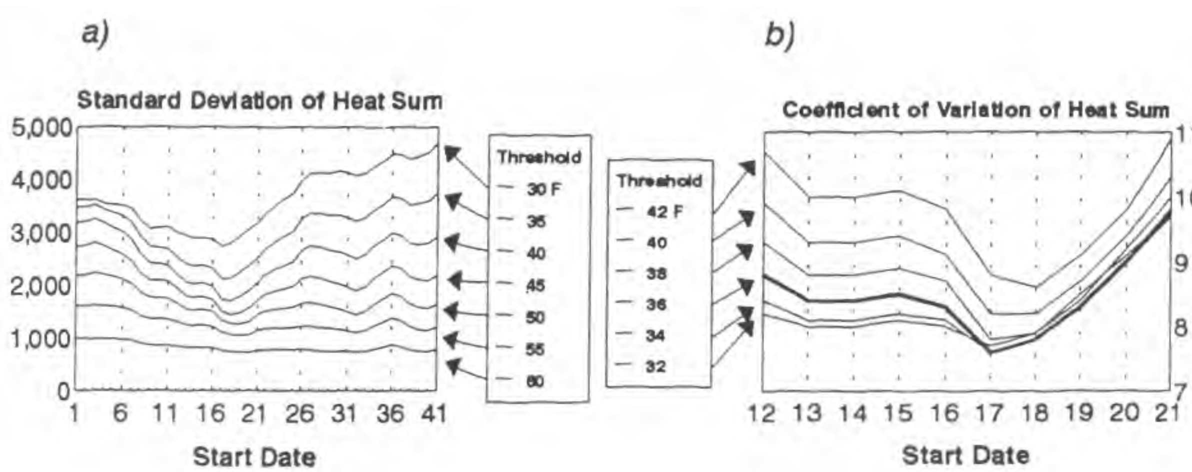

shedding in 1992 and is consistent with a heatsum model. The difference in timing of stage 5.5 between the coolest year (1988) and the warmest year (1990) for a given clone was greater than the between clone variation within years and ranged from 16 to 31 days with a mean of 23 days.

Once these target dates had been established, the heat sum at which PDCS stage 5.5 was reached was determined for a model with a given threshold and start date, and the standard deviation and coefficient of variation of the heat sums for the four years were calculated. This process was repeated for 'all combinations of threshold and start date. The effect of varying the parameters is shown in figure 2. Figure 2a shows PDCS scores for clone 19 plotted against heat sums based on a start date of January 1 and a threshold of 50 degrees F. With this model, score 5.5 was reached at a lower heatsum in 1988 even though this was the coldest, latest year. Boyer described a similar relationship, *i.e.* lower heat sums required when development times were longer, but this relationship could be modeled in our study by lowering the threshold temperature and assuming a constant critical heat sum over years. Figure 2b shows that a change of threshold from 50 to 40 degrees has "pulled in" the critical heat sum for 1988. This *is* because addition of heat units between 40 and 50 degrees occurs over a longer period of time in 1988.

The results of the parameter grid search for one clone are presented in figure 3. In figure 3a, the standard deviation increases with decreasing threshold because the heat sums are larger. However, for a given threshold, the minimum s.d. indicates the best start date. For clone 19, this best date is between day 17 and 20, depending on the threshold. No other minima were found outside the range shown in the graph so we are confident that the best start date occurs after January 1. Plots of s.d. for other clones showed similar patterns and optimal start dates. Figure 3b shows the coefficient of variation for the different models. An increase in the threshold results in higher a c.v. because differences in temperature become relatively more important. These curves are roughly parallel, but note the line for threshold = 36: for a start date after day 17, the c.v. is actually lower than for a threshold of 32 or 34. This is an indication that 36 is *the* best choice to reduce the variation in heat sum required to reach PDCS stage 5.5 for this clone. Some clones were fairly insensitive to changes in threshold or start date, but most showed a reduction in s.d. and c.v. with a threshold near 36 degrees Fahrenheit and a start date near day January 17, so these parameters were chosen to represent the entire orchard. Figure 3c shows the PDCS score curves using this model.

TABLE 3. Observed and predicted Julian dates and residual days that clones of Loblolly pine reached PDCS stage 5.5 using a heat sum model with a start date of Jan. 1 and a threshold of 36 F.

Clone	1988			1989			1990			1991			1992		
	Obs	Pred.	Res	Obs	Pred.	Res	Obs	Pred.	Res	Obs	Pred.	Res	Obs	Pred.	Res
53	70	77	-7	-	-	-	54	55	-1	64	64	0	67	63	4
22	78	80	-2	-	-	-	-	-	-	66	65	1	65	65	0
43	83	82	1	-	-	-	52	61	-9	72	67	5	68	66	2
28	83	83	0	-	-	-	55	61	-6	72	68	4	68	67	1
00	81	82	1	65	72	-7	57	60	-3	73	67	6	68	66	2
33	81	83	-2	71	73	-2	60	61	-1	73	68	5	68	67	1
39	85	85	0	74	75	-1	63	64	-1	75	72	3	69	69	0
20	86	86	0	74	75	-1	65	65	0	75	72	3	68	70	-2
19	86	87	-1	76	76	0	63	67	-4	79	74	5	70	71	-1
37	87	87	0	75	76	-1	64	67	-3	77	74	3	70	71	-1
73	87	87	0	-	-	-	64	67	-3	77	74	3	70	71	-1
31	88	90	-2	78	79	-1	70	70	0	82	77	5	71	77	-6
Average			-1			-2			-3			4			0

Table 3 shows the difference between observed and predicted dates of reaching stage 5.5 for twelve clones using this model. The residual between observed and predicted dates was only one or two days for most clones in most years. Exceptions seem to be early clones ("53" and "00") that flower much earlier than predicted in some years. Average residual was three days early in 1990. This year was a warmer than the rest and our model did not completely account for the difference. In 1991, the residuals were four days "late". We believe that this is due to an unusual cold snap that occurred in mid February of that year. In its simple form, a heat sum model does not account for any developmental setback that may occur from cold weather. Residuals were low for 1992, the independent year, indicating that our model may be useful for predicting pollen development in future years. However , these accurate predictions are due in part to the fast speed at which pollen matured from stage 4.0 to 5.5 in 1992.

CONCLUSIONS

Our results indicate that the selected heat sum model should be useful for predicting pollen shedding for the study location. Ramets of the same clone develop at the same time and rate, so clones can be represented by a single ramet. Pollen develops faster in warm years, indicating a relation to temperature and development. A heat sum model with a threshold of 36 degrees F. and a start date of Jan 17 reduced the s.d and c.v. for most of the clones. The accuracy of the model is not highly sensitive to these parameters and may vary if a different data set is used. Predicting the timing of pollen shedding seems feasible, but less so for very early or late clones, and years with unusually cold or warm periods during pollen maturation may reduce the accuracy of the predictions.

Orchard managers need not make detailed observations of pollen development to use a heat sum model for predicting shedding. A record of the timing of a certain observable event (e.g. the beginning of pollen release for a single clone) along with temperature data over several years would be adequate data for rudimentary model develpment.

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