SECTION IV: IMPLEMENTATION OF ANNUAL VARIABILITY IN THE MASTING MODEL

IV.1 INTRODUCTION

Spatial variation accounts for only a small part of the variation in mast production. The essence of masting behavior and the basis for many of the theories regarding the evolution of masting behavior is the variation that occurs among years (LaLonde and Roitberg 1992, Waller 1979, Silvertown, 1980, Koenig *et al*. 1994). In this section, I take the output mast indices from the spatial model, MAST, and using land type, climate, disturbance variables, and interactions among years, simulate the influence these variables may have on mast production for a ten-year period. As with the description of the development and algorithm for the spatial model, I will describe and justify parameters and relationships by referring to a schematic of the annual model and a partial listing of the program code (Figure IV.1; and Table IV.1). The figure is self-explanatory, however the table requires some explanation.

The partial listing of the program code is about 7 pages in length. The first two pages deal with assigning values to coefficient variables used later in the model. The next two pages list the code for year 0 of the simulation. The model factors interactions between years (*e.g.* red oak flowers develop in one year but the acorns develop the following year, and a high level of mast production one or two years in a row might limit resources for mast production following years). Therefore, the algorithm for the first year of simulation (year 0) differs from subsequent years since information is not available for year n-1 and n-2. For Year 0, a random number generator is utilized for factoring the

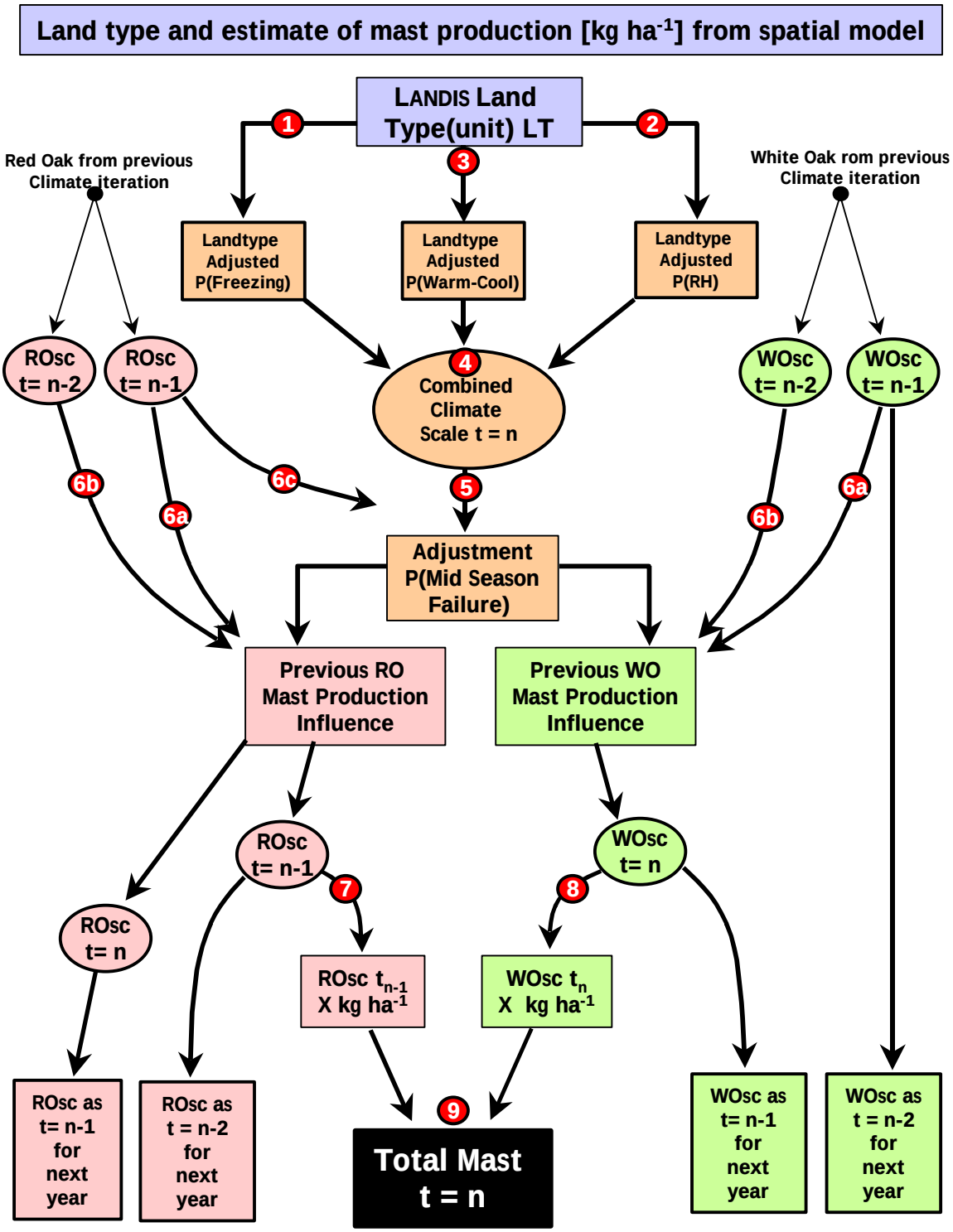

Figure IV.1 The algorithm for adding annual variability in mast production to the spatial variation model: MAST. Circled numbers are description references for functional relationships.

Table IV.1 A partial listing of the model adding annual variation to the spatial mast model the entire model is iterative and is approximately 1200 lines in length. References in the text regarding procedure descriptions are noted for year 1 of the model (below).

```
/*   Do file for manipulating spatial mast model for temporal (annual) variabiity    */
/*   Last update 13 Jan 2001                                                          */

* Previous recent (N-1 ) mast production influence factors (slope and intercept)

        local    ynm1_sl  = -1.80
        local    ynm1_in  = 1.15

* Previous recent (N-2) mast production influence factors (slope and intercept)

        local    ynm2_sl  = -2.40
        local    ynm2_in  =  2.00

* Coefficients for influence of land type on climate factors

    /* Freeze */

        local fr_1_sl = -10.00     /* Slope coefficient for influence of Land Type 1 on freeze potential      */
        local fr_1_in =   9.00     /* Intercept coefficient for influence of Land Type 1 on freeze potential  */
        local fr_2_sl =  -5.56     /* Land Type 2  etc..                                                      */
        local fr_2_in =   4.88
        local fr_3_sl =  -8.33     /*  if generated values >1 then reset to 1.00 below                        */
        local fr_3_in =   7.50     /*  if generated values <0 then reset to 0.00 below                        */
        local fr_4_sl =  -6.67
        local fr_4_in =   6.00
        local fr_5_sl =  -4.35
        local fr_5_in =   3.83
        local fr_6_sl =  -6.67
        local fr_6_in =   6.00
        local fr_7_sl =  -6.67
        local fr_7_in =   6.00
```

/* Relative humidity */

```
local rh_1_sl =  -3.33        /* Slope coefficient for influence of Land Type 1 on low RH potential        */
local rh_1_in =   2.33        /* Intercept coefficient for influence of Land Type 1 on freeze potential    */
local rh_2_sl =  -2.22        /* Land Type 2  etc..                                                        */
local rh_2_in =   1.56
local rh_3_sl =  -3.33        /*  if generated values >1 then reset to 1.00 below                          */
local rh_3_in =   2.33        /*  if generated values <0 then reset to 0.00 below                          */
local rh_4_sl =  -2.50
local rh_4_in =   1.75
local rh_5_sl =  -2.00
local rh_5_in =   1.40
local rh_6_sl =  -2.50
local rh_6_in =   1.75
local rh_7_sl =  -2.50
local rh_7_in =   1.75
```

/* Warm cool temperature regime */

```
local wc_b_sl =  -0.85        /* Same for all land types                                                   */
local wc_b_in =   1.12
```

*** Prob. of mid-season external biotic and abiotic factors**

```
*                    Note: no literature references re: p(values)

/*  Insect outbreaks, hailstorms, drought, dry flower-desiccating winds          */
/*  One in ten years, 80 percent failure due to one of these factors  1-(1/7) = 0.85   */

local failure = 0.85          /* threshold for failure frequency                 */
local failper = 0.20          /* fraction of acorns surviving                    */

local y0_fail = uniform()     /* Random # for p of non-failure    Year 0         */
local y1_fail = uniform()     /* Random # for p of non-failure    Year 1         */
:
:
local y10fail = uniform()
```

*** YEAR 0 (calculated for red oak group inclusion in mast index for year 1)**

```
local   y0_fr  =  uniform()        /*  p(favorable freezing) - (i.e. no freezing events)                    */
local   y0_rh  =  uniform()        /*  p(favorable RH) - several days with low daytime rh                   */
local   y0_wc  =  uniform()        /*  p(temperature regime)- warm-cool for pollination synchrony           */
```

*** Freeze influence scale generator by land type**

```
                                                   /*  Freeze probability ---> to scale          */
gen fr_sc_y0 =     ( `fr_1_sl' *  `y0_fr' )+ `fr_1_in'        if land ==1
replace fr_sc_y0 = ( `fr_2_sl' *  `y0_fr' )+ `fr_2_in'        if land ==2
replace fr_sc_y0 = ( `fr_3_sl' *  `y0_fr' )+ `fr_3_in'        if land ==3
replace fr_sc_y0 = ( `fr_4_sl' *  `y0_fr' )+ `fr_4_in'        if land ==4
replace fr_sc_y0 = ( `fr_5_sl' *  `y0_fr' )+ `fr_5_in'        if land ==5
replace fr_sc_y0 = ( `fr_6_sl' *  `y0_fr' )+ `fr_6_in'        if land ==6
replace fr_sc_y0 = ( `fr_7_sl' *  `y0_fr' )+ `fr_7_in'        if land ==7

replace fr_sc_y0 = fr_sc_y0 + 0.04 * (invnorm(uniform()))     /* random variability */

replace fr_sc_y0 = 0 if fr_sc_y0 < 0.01                       /* reset to 0 if scale =f(random) < 0        */
replace fr_sc_y0 = 1 if fr_sc_y0 >1.000                       /* reset to 1 if scale =f(random) > 1        */
format  fr_sc_y0        %9.3f
```

*** Relative humidity influence scale generator by land type**

```
                                                   /*  Relative humidity ---> to scale           */
gen     rh_sc_y0 = ( `rh_1_sl' *  `y0_rh' )+ `rh_1_in'        if land ==1
replace rh_sc_y0 = ( `rh_2_sl' *  `y0_rh' )+ `rh_2_in'        if land ==2
replace rh_sc_y0 = ( `rh_3_sl' *  `y0_rh' )+ `rh_3_in'        if land ==3
replace rh_sc_y0 = ( `rh_4_sl' *  `y0_rh' )+ `rh_4_in'        if land ==4
replace rh_sc_y0 = ( `rh_5_sl' *  `y0_rh' )+ `rh_5_in'        if land ==5
replace rh_sc_y0 = ( `rh_6_sl' *  `y0_rh' )+ `rh_6_in'        if land ==6
replace rh_sc_y0 = ( `rh_7_sl' *  `y0_rh' )+ `rh_7_in'        if land ==7

replace rh_sc_y0 = rh_sc_y0 + 0.04 * (invnorm(uniform()))     /* random variability */

replace rh_sc_y0 = 0 if rh_sc_y0 <0.01                        /* reset to 0 if scale =f(random) < 0 = total negative influence      */
replace rh_sc_y0 = 1 if rh_sc_y0 >1.000                       /* reset to 1 if scale =f(random) > 1  = No influence                 */
format  rh_sc_y0        %9.3f
```

```
* Standard temperature sequence (wc) influence scale generator

gen wc_sc_y0 = ( `wc_b_sl' *  `y0_wc' )+ `wc_b_in'

        replace wc_sc_y0 = wc_sc_y0 + 0.04 * (invnorm(uniform()))      /* random variability                    */

        replace wc_sc_y0 = 0 if wc_sc_y0 <0.01                         /* reset to 0 if scale =f(random) < 0    */
        replace wc_sc_y0 = 1 if wc_sc_y0 >1.000
                format  wc_sc_y0       %9.3f

* Generate climate effect scale = product of freeze, rh, and warm-cool scales

gen y0_scale = fr_sc_y0 * rh_sc_y0 * wc_sc_y0

* Adj. for prior mast production influence on year[0] red oak by          (0 to 1) random # for n-1  & n-2 influence

        /* Previous years n=(0-1) and n=(0-2) random # for ro scale in year 0    */

local  y0_2sc = uniform()
local  y0_1sc = uniform() * ((`ynm1_sl' * `y0_2sc' ) +`ynm1_in' )      /* n-1 affected by n-2 rand. mast scale  */
replace y0_scale = y0_scale * ((`ynm1_sl' * `y0_1sc' ) +`ynm1_in' )
replace y0_scale = y0_scale * ((`ynm2_sl' * `y0_2sc' ) +`ynm2_in' )
        replace y0_scale = 1 if y0_scale > 1.00
        replace y0_scale = 0 if y0_scale < 0.00

gen y0_rosc = y0_scale
gen y0_wosc = y0_scale
        format       y0_scale  %9.3f
```

*** YEAR 1**

```
local   y1_fr  =  uniform()        /* Random # for probability of favorable freezing (i.e. no freezing events)                    */
local   y1_rh  =  uniform()        /* Random # for prob. of favorable RH - several days with low daytime rh                      */
local   y1_wc  =  uniform()        /* Random # for prob. of favorable temp. regime warm-cool for pollination synchrony            */
```

1,2,3

*** Freeze influence scale generator by land type**

```
gen fr_sc_y1 =     ( `fr_1_sl' *  `y1_fr' )+ `fr_1_in'        if land ==1
replace fr_sc_y1 = ( `fr_2_sl' *  `y1_fr' )+ `fr_2_in'        if land ==2
replace fr_sc_y1 = ( `fr_3_sl' *  `y1_fr' )+ `fr_3_in'        if land ==3
replace fr_sc_y1 = ( `fr_4_sl' *  `y1_fr' )+ `fr_4_in'        if land ==4
replace fr_sc_y1 = ( `fr_5_sl' *  `y1_fr' )+ `fr_5_in'        if land ==5
replace fr_sc_y1 = ( `fr_6_sl' *  `y1_fr' )+ `fr_6_in'        if land ==6
replace fr_sc_y1 = ( `fr_7_sl' *  `y1_fr' )+ `fr_7_in'        if land ==7
replace fr_sc_y1 = fr_sc_y1 + 0.04 * (invnorm(uniform()))     /* random variability */
replace fr_sc_y1 = 0 if fr_sc_y1 < 0.01                       /* reset to 0 if scale =f(random) < 0      */
replace fr_sc_y1 = 1 if fr_sc_y1 >1.000                       /* reset to 1 if scale =f(random) > 1      */
format  fr_sc_y1        %9.3f
```

1

*** Relative humidity influence scale generator by land type**

```
gen     rh_sc_y1 = ( `rh_1_sl' *  `y1_rh' )+ `rh_1_in'        if land ==1
replace rh_sc_y1 = ( `rh_2_sl' *  `y1_rh' )+ `rh_2_in'        if land ==2
replace rh_sc_y1 = ( `rh_3_sl' *  `y1_rh' )+ `rh_3_in'        if land ==3
replace rh_sc_y1 = ( `rh_4_sl' *  `y1_rh' )+ `rh_4_in'        if land ==4
replace rh_sc_y1 = ( `rh_5_sl' *  `y1_rh' )+ `rh_5_in'        if land ==5
replace rh_sc_y1 = ( `rh_6_sl' *  `y1_rh' )+ `rh_6_in'        if land ==6
replace rh_sc_y1 = ( `rh_7_sl' *  `y1_rh' )+ `rh_7_in'        if land ==7
replace rh_sc_y1 = rh_sc_y1 + 0.04 * (invnorm(uniform()))     /* random variability                      */
replace rh_sc_y1 = 0 if rh_sc_y1 <0.01                        /* reset to 0 if scale =f(random) < 0      */
replace rh_sc_y1 = 1 if rh_sc_y1 >1.000                       /* reset to 1 if scale =f(random) > 1      */
format  rh_sc_y1        %9.3f
```

2

*** Standard temperature sequence (wc) influence scale generator**

```
gen wc_sc_y1 = ( `wc_b_sl' *  `y1_wc' )+ `wc_b_in'

        replace wc_sc_y1 = wc_sc_y1 + 0.04 * (invnorm(uniform()))          /* random variability   */

 replace wc_sc_y1 = 0 if wc_sc_y1 <0.01                  /* reset to 0 if scale =f(random) < 0        */
 replace wc_sc_y1 = 1 if wc_sc_y1 >1.000                 /* reset to 1 if scale =f(random) > 1        */
        format  wc_sc_y1       %9.3f
```

3

*** Generate climate effect scale = product of freeze, rh, and warm-cool scales**

```
gen y1_scale = fr_sc_y1 * rh_sc_y1 * wc_sc_y1
```

4

*** Mid-season failure events**

```
replace y1_scale = y1_scale * `failper' if (`y1_fail' > `failure')     /* Current year influence  on WO fl/ac & RO fl     */
replace y0_rosc  = y0_rosc  * `failper' if (`y1_fail' > `failure')     /* Current year influence  on RO acorns            */

gen y1_rosc = y1_scale                                                 /* Current year influence  scale for RO            */

gen y1_wosc = y1_scale                                                 /* Current year influence  scale for WO            */
```

5

*** Factor the influence of the previous years mast production**

```
/* t - 1 = year 0*/

        replace y1_rosc = y1_rosc * (y0_rosc * `ynm1_sl' + `ynm1_in')
                replace y1_rosc = 1 if y1_rosc > 1.00
                replace y1_rosc = 0 if y1_rosc < 0.00

        replace y1_wosc = y1_wosc * (y0_wosc * `ynm1_sl' + `ynm1_in')
                replace y1_wosc = 1 if y1_wosc > 1.00
                replace y1_wosc = 0 if y1_wosc < 0.00
```

6a

```
/* t -2  = year -1*/

        replace y1_rosc = y1_rosc * (`y0_1sc' * `ynm2_sl' + `ynm2_in')
                replace y1_rosc = 1 if y1_rosc > 1.00
                replace y1_rosc = 0 if y1_rosc < 0.00

        replace y1_wosc = y1_wosc * (`y0_1sc' * `ynm2_sl' + `ynm2_in')
                replace y1_wosc = 1 if y1_wosc > 1.00
                replace y1_wosc = 0 if y1_wosc < 0.00
                        format      y1_scale  %9.3f
```

6b

*** Generate current year (1) mast production**

```
gen y1romst = kg_ro90 * y0_rosc                    /* Red oak mast maturing Year 1      */

gen y1womst = kg_wo90 * y1_wosc                    /* White Oak mast maturing Year 1    */

gen y1_mast = y1romst + y1womst                    /* Total Mast Production             */
```

7

8

9

*** similar calculations for each of simulation years 2 through 10**

influences of preceding mast production. The algorithm for simulation Years 1 through 10 are the same and show the interactions among years, therefore the last three pages of the Table IV.1 list the code for Year 1 and the notations in the left margin link the table to the schematic and to the text description below.

IV.2 METHODS: MODEL DEVELOPMENT

IV.2.1 Model development: Input variables

Only some of the information generated by the spatial model is utilized in the annual model. For each cell, the Land Type classification and the potential mast index value (sum of tree mast index values) generated by the spatial model is used to estimate realized mast production in the annual model. Although the mast index values are indices, they are roughly equivalent to a more tangible measure, kg ha^{-1}. In all figures and tables the two "measures" are used interchangeably and are equivalent.

IV.2.2 Model development: Climate variables

In Section II.4, I presented the results of a brief (and subjective) evaluation of historical climate data from the perspective of mast production. The climate variables considered are freezing temperatures, relative humidity and a warm-cool temperature regime during and after pollination with respect to flowering success. Flowering success, as I define it, involves the successful release of pollen, airborne transport of pollen, deposition of viable pollen on pistillate flowers, pollen germination and ovule fertilization. From the examination of the historical climate data, I developed an opinion

about the probability of the occurrence of mast-influencing events (Table IV.2). My subjective examination of the statewide daily minimum temperature plots (Figure II.24) produced the estimated probability that in 1 of every 5 years (20%), there is potential for a flower damaging spring freeze (Table IV.2). Sharpe and Sprague (1967) estimated that mast-influencing spring freezes occurred in only 8 percent of the 50 years on record for a study in Pennsylvania. The data available for Missouri include only the daily minimum temperature; thus, the duration of the below-freezing temperature is not known. In addition, although temperature did reach a low level with potential for damage, it is not known at what stage of development the oak flowers were and how vulnerable they were at the time of the low temperature. For these reasons, the base level for the probability of favorable (no-freeze) conditions was set at 90 percent. That is, any number below 0.90 generated by a random number utility results in no reduction in mast production for that year.

Relative humidity influences masting by interfering with the distribution of pollen; i) by inhibiting the opening of anthers and release of pollen from staminate flowers, ii) by limiting the transport of pollen by acting as humidity nucleating "seeds" and precipitating from the atmosphere (Figure II.25) , iii) by causing flowers and pollen to decay during long periods of high humidity, iv) or all these factors combined. Historical relative humidity data were interpreted in a manner similar to that of minimum temperature, although a range of potential impacts of relative humidity was noted during the evaluation (negative, positive and favorable). The negative classification was assigned to years when daytime relative humidity remained high for most of the critical flowering period (April 15th to May 15th). The positive designation was assigned to years

Table IV.2 Subjective rankings of favorable or unfavorable climate conditions for recording stations throughout Missouri and base values applied to the landscape. Negative implies a negative impact on potential mast production and positive implies the opposite. Favorable indicates the fraction of years viewed to display markedly positive conditions for that climate variable.

Review of Historical Climate Data

			Number of Years Reviewed	Negative	Positive	Favorable
Relative Humidity	**St. Louis**	**Count**	33	13	16	3
		Fraction		0.39	0.48	0.09
	Columbia Springfield	**Count**	62	30	21	11
		Fraction		0.48	0.34	0.18
Potentially Freezing Temperature	**Throughout Missouri**	**Count**	86	17		
		Fraction		0.20		
Warm/Cool Temperature Sequence	**Throughout Missouri**	**Count**	86		13	
		Fraction			0.15	

Mean Probabilities used in the masting model

	Probability of a Favorable Year				Favorable Year Return Interval [years]
	Freeze[1]	**RH**	**Warm-cool[2]**	**Product**	
Base	0.90	0.50	0.30	0.14	7.4

1. For Missouri 17 of 86 (20%) of the years reviewed a sub -1 C event occurred between April 15th and May 14th. The base value used reflects the possibility of male and or female flowers not being susceptible during freeze events.

2. About 15 percent of the 86 years reviewed were judged to have positive or favorable temperature sequences conditions for flower success. The base value used (30%) reflects the uncertainty of the timing of flowering, interpretation of historical records, and reality of the influence.

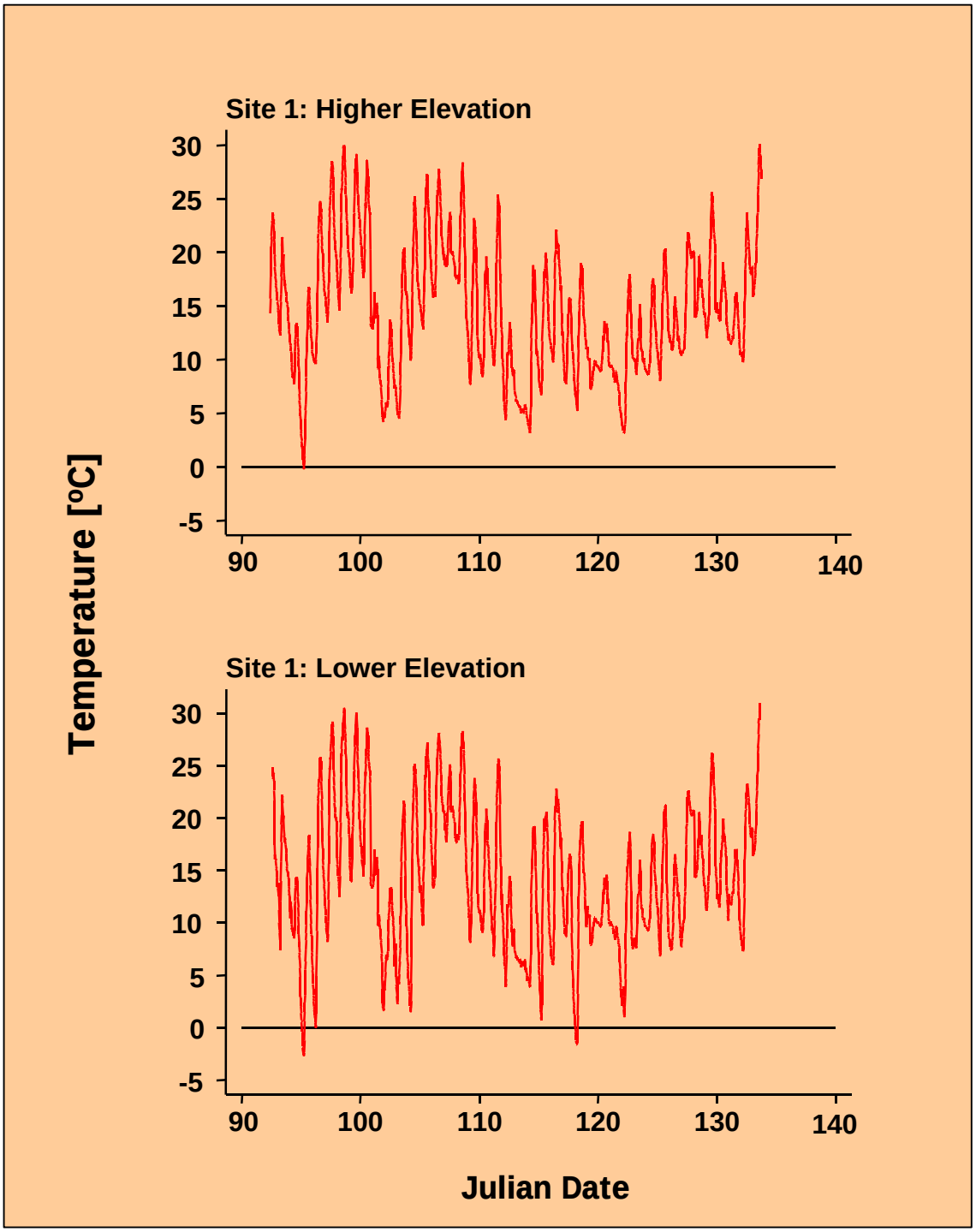

Figure IV.2 The difference in temperature among topographic positions during the 1995 oak flowering period . The difference in elevation between these northeast facing sites in southern Missouri is about 100m (Haenchen and Larsen, unpublished data)

when relative humidity was at times low enough to allow successful pollination and the favorable classification was assigned to years when there were extended periods with daytime relative humidity below 50 percent. A base probability level of 0.50 was assigned to the relative humidity parameters. The influence of relative humidity and variation that may occur within a canopy and among sites is discussed below.

A warm-cool spring temperature regime has been proposed as a positive factor affecting mast production (Sharp and Chisman, 1961; Sork *et al*. 1993) and was estimated to occur during only 13 of the 86 years reviewed (15 percent). The potential influences of freezing temperatures and high relative humidity are more easily verified for the influence on mast production than a warm-cool regime. For this reason, the probability level set for a warm-cool temperature regime was set at 0.30 and the effect of this regime is not as complete. That is, the lack of a warm-cool temperature regime never completely eliminated the acorn crop.

The combined probability of favorable climate conditions could be calculated by multiplying these three probabilities, i.e.

$$0.90 \times 0.50 \times 0.30 = 0.14$$

Thus, favorable conditions are estimated to occur in 14 percent of years. Another way of expressing this is that the return interval for good mast crop years is 7.4 years (1/0.14).

IV.2.3 Model development: Microclimate variables and spatial variability

Microclimate varies with topographic position. Figure IV.2 shows the difference in temperature regimes for two sites on a northeast slope that differed by about 100 m in elevation in southern Missouri. As is shown, on one occasion the higher elevation site

nearly reached a low temperature of 0 ^{o}C, whereas on two dates, the temperature was below 0 ^{o}C. Simultaneous measurements of relative humidity showed little difference between the lower and higher elevation sites (Figure IV.3). In contrast, climate data recorded at two nearby sites on an eastern slope in North Carolina also differing by approximately 100 meters in elevation show that the lower elevation site had relative humidity levels often more than 15 percent lower than the higher elevation site (Figure IV.4). The method of applying these probabilities in the model and accounting for topographic influences is described below.

IV.2.4. Model development: Climatic influences and scaling factors

For each of the seven land types, a subjective judgment was made with respect to the potential impact the climate might have on each climate variable and a sites mast production. Perhaps the clearest example of this method is that for freezing. In Step 1 of the model schematic (Figure IV.1), the probability of a freezing event and the impact of land type on the influence that this probability has on masting is estimated. First, a random number (0-1) is generated. For all land types, if the random number is >0.90, then the effect on that year's flower crop is severe and a scale factor is generated that reduces the flower crop to 0, i.e. the scale factor is 0 due to a simulated hard freeze during flower development. However, freezing events would not be expected to occur at the same frequency or for the same duration on all land types. For example, freezing temperatures may occur more frequently on upland drainage sites (Land Type 5), and longer periods of these low temperatures may result in a lower mast production rate. The random number is used to stochastically factor these differences. A scale factor is

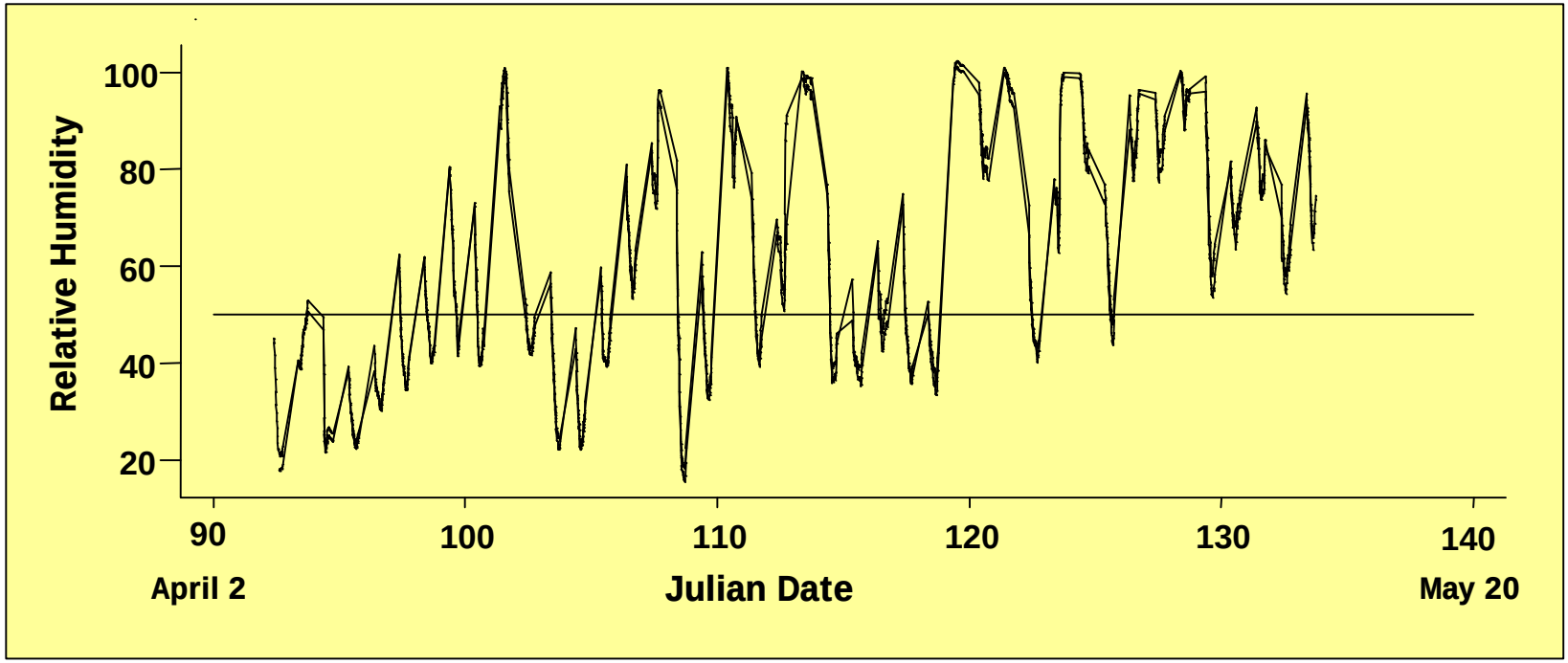

Figure IV.3 Daytime (0900 to 1800) relative humidity recorded at two elevations (~84 m vertical difference) on MOFEP sites in 1995. Observations were recorded at 20 minute intervals (Haenchen and Larsen; unpublished data).

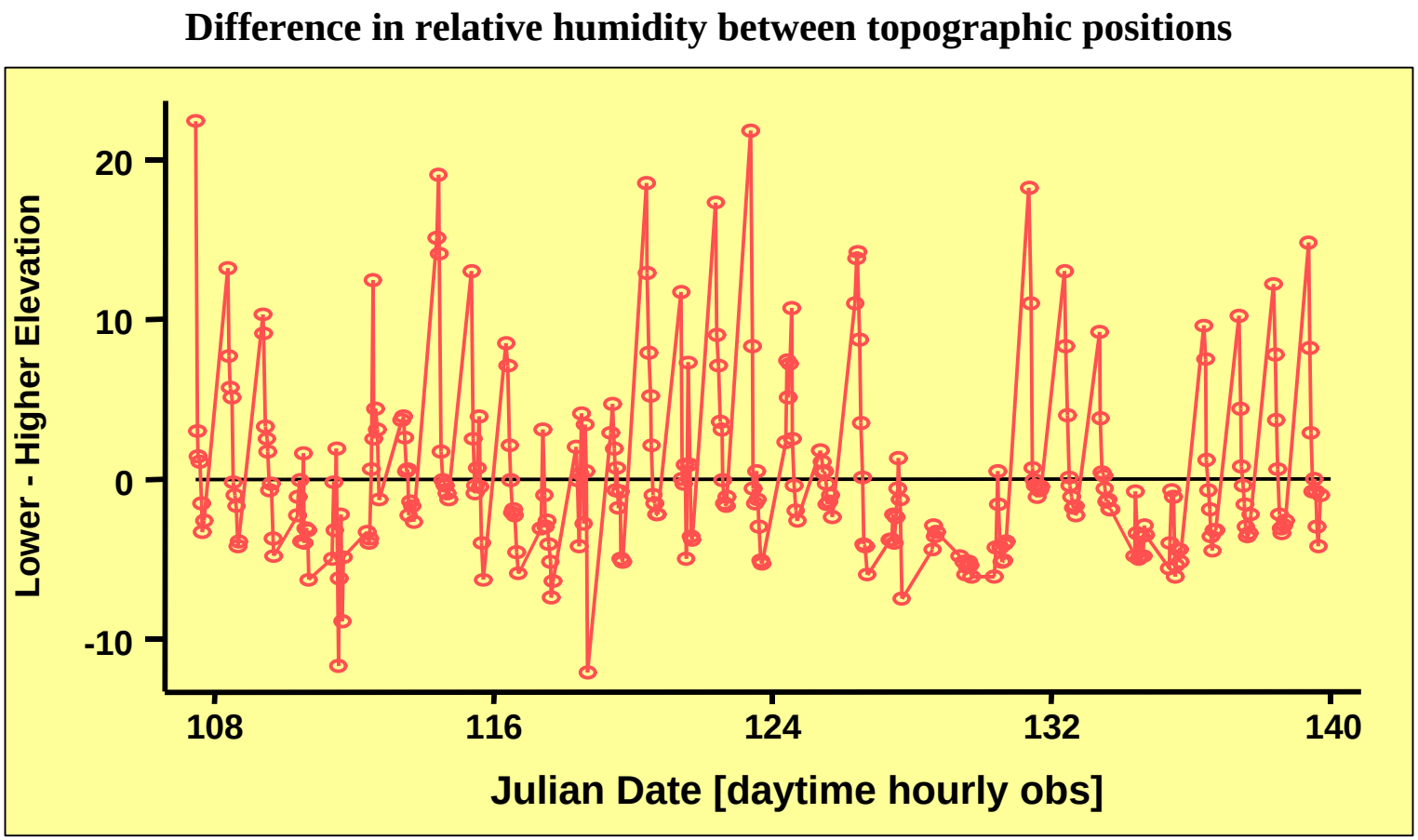

Figure IV. 4 The influence of topographic position on concurrent relative humidity between two low elevation sites (740and 840 m) in the southern Appalachian mountains (North Carolina) during daytime hours (0900 to 1800) between April 18th and May 18th, 1992. Observations were recorded hourly above canopy (N.H. Sullivan, unpublished data).

generated for freezing based on the relationships shown in Figure IV.5. These straight line segments are generated first by entering the random number into a simple linear function to generate a scale factor and then reassigning a scale factor of 1 to all generated scale factors >1 and 0 to all scale factors < 0 leaving all scale factors between 0 and 1 and a function with three line segments. The slope and intercept coefficients differ for each land type and are listed in Table IV.3. Lower negative slope values (or higher intercept values) indicate land types that are expected to be less susceptible to frost damage to flower crops. I judged land types 4,5, and 7 (Glade, Mesic, and Limestone) as equivalent and moderate in damage potential. Upland drainages (Type 5) were considered the most susceptible, with North and East slopes more susceptible than average but less susceptible than Upland Drainage sites. The least susceptible sites are South- and West-slopes.

A similar routine is repeated for relative humidity (Schematic Figure IV.1 and Table IV.1: reference 2). Since favorable relative humidity conditions are less frequent the mean value is near the middle of the figure. Since unfavorable conditions were estimated to occur more (about 30 percent of the time; Table IV.2), random numbers greater than about 0.7 result in no flowering success. The gradient between completely favorable (scale factor 1) and completely unfavorable (scale factor 0), is more gradual and varies among land types. Again, Upland Drainages and N & E slopes are viewed as more susceptible to high relative humidity. The difference in the slopes among the land types reflects judgement regarding both the probability of favorable relative humidity in general and the duration of favorable conditions. Oak flowers require several hours of low relative humidity to release pollen (Wolgast and Stout 1977).

Table IV.3 Parameters used to generate scale factors based on the probability of favorable climate conditions. The [x at y=1] column indicates the probability threshold level when the climate factor has no influence on the masting index and the [x at y=0] column indicates the probability threshold when the climate factor is severe enough to reduce the masting index to 0.

			x at y = 1 intercept	x at y = 0 intercept	Scale factor Calculation slope	const
Freeze	**Base**[1]		0.75	0.90	-6.67	6.00
	1	**S & W**	0.80	0.90	-10.00	9.00
	2	**N& E**	0.70	0.88	-5.56	4.88
	3	**Ridge/Flat**	0.78	0.90	-8.33	7.50
	4	**Glade/Savanna**	0.75	0.90	-6.67	6.00
	5	**Upland Drainage**	0.65	0.88	-4.35	3.83
	6	**Limestone**	0.75	0.90	-6.67	6.00
	7	**Mesic**	0.75	0.90	-6.67	6.00
RH	**Base**		0.30	0.70	-2.50	1.75
	1	**S & W**	0.40	0.70	-3.33	2.33
	2	**N& E**	0.25	0.70	-2.22	1.56
	3	**Ridge/Flat**	0.40	0.70	-3.33	2.33
	4	**savanna/Glade**	0.30	0.70	-2.50	1.75
	5	**Upland Drainage**	0.20	0.70	-2.00	1.40
	6	**Limestone**	0.30	0.70	-2.50	1.75
	7	**Mesic**	0.30	0.70	-2.50	1.75
WC		**All**			-0.79	1.24

1. Base values are listed and calculated to reduce the number of calculations. Land type 4, 5, and 7 are assigned the base values.
2. The scale factor is generated from a (0-1) uniform random distribution. Generated scale values greater than 1.00 are reset to 1 and generated values less than 0.00 are reset to 0.

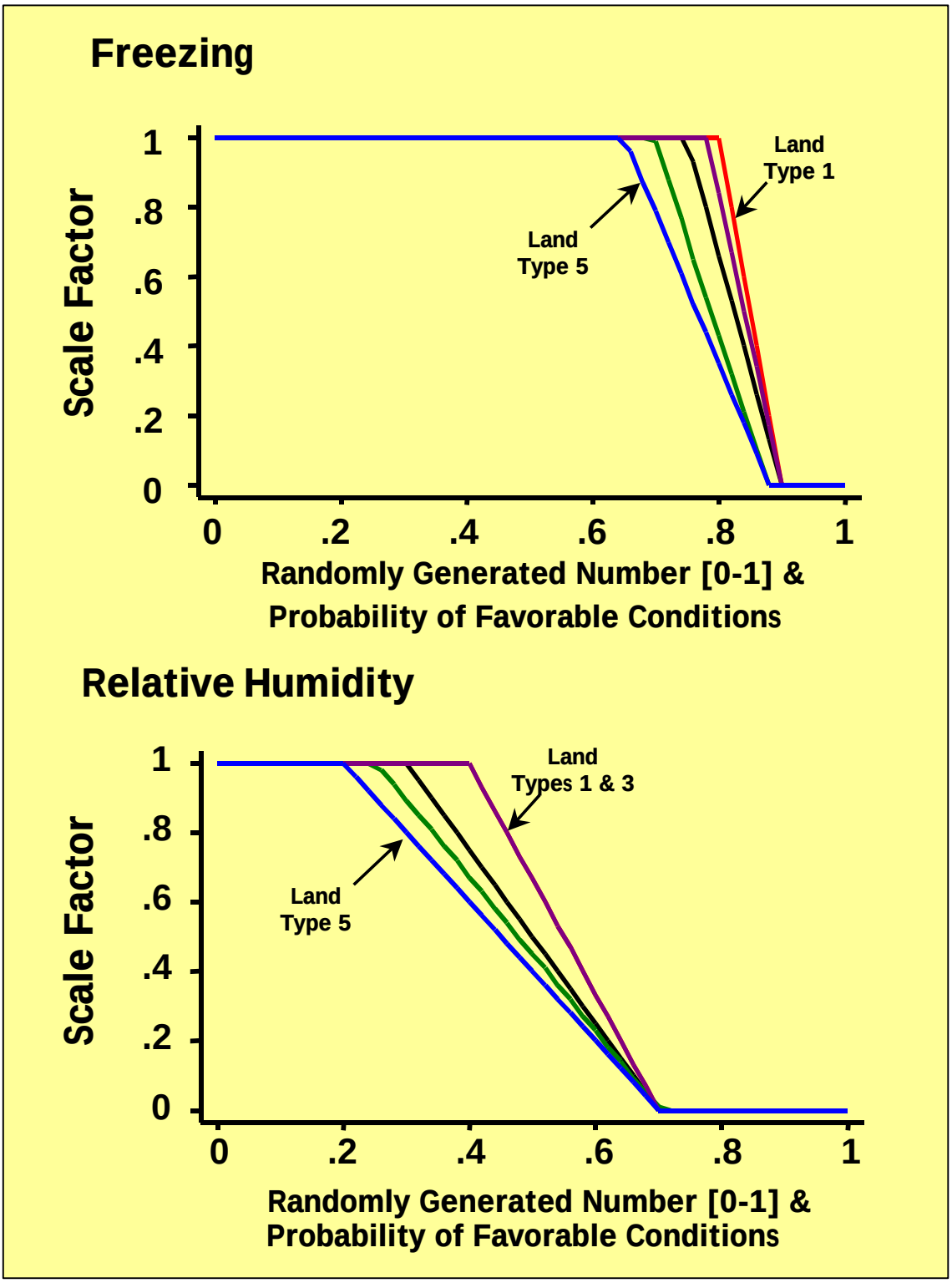

Figure IV.5 Influence of climate factors on mast index. A random number is generated and the influence of the factor (scale multiplier) is derived from the relationships shown.

The random number generated for the warm-cool temperature effect produced a scale factor that is not as influential on flowering success as that for relative humidity or freezing (Figure IV.6; Schematic: Code reference 3). It does factor a probability of completely favorably conditions for about 20 percent of the years, but there is a gradual effect on mast production and the scale factor never falls below 0.35. The product of these three climate variable factors is calculated as single combined, scaling factor (Table IV.1 and Schematic reference 4) for each cell.

IV.2.5 Model development: Random mid-season crop failure

Temperature, relative humidity, and the warm-cool temperature regime during the flowering period are not the only factors that affect mast production. Hailstorms, insect outbreaks, predation, and drought among other periodic events throughout the growing season also affect mast production. Although, I do not have quantitative data to support this adjustment or calculate probabilities, I have set the probability level for one of these serious events at once in seven years and that the scale factor is reduced by 80 percent (Table IV.1, reference 5). A generated random number of less than < 0.85 multiplies the scale factor by 1 and a random number of greater than 0.85 results in the scale factor being multiplied by 0.20. Of course, hailstorms and insect outbreaks may not affect the entire landscape and drought would not affect an entire landscape equally; however, I felt these factors should be considered.

In addition to the current year's white oak flower population, the red oak flower population from the previous year is influenced by the random mid-season influences (Schematic reference 6c). The current year red oak flower crop is not influenced by these

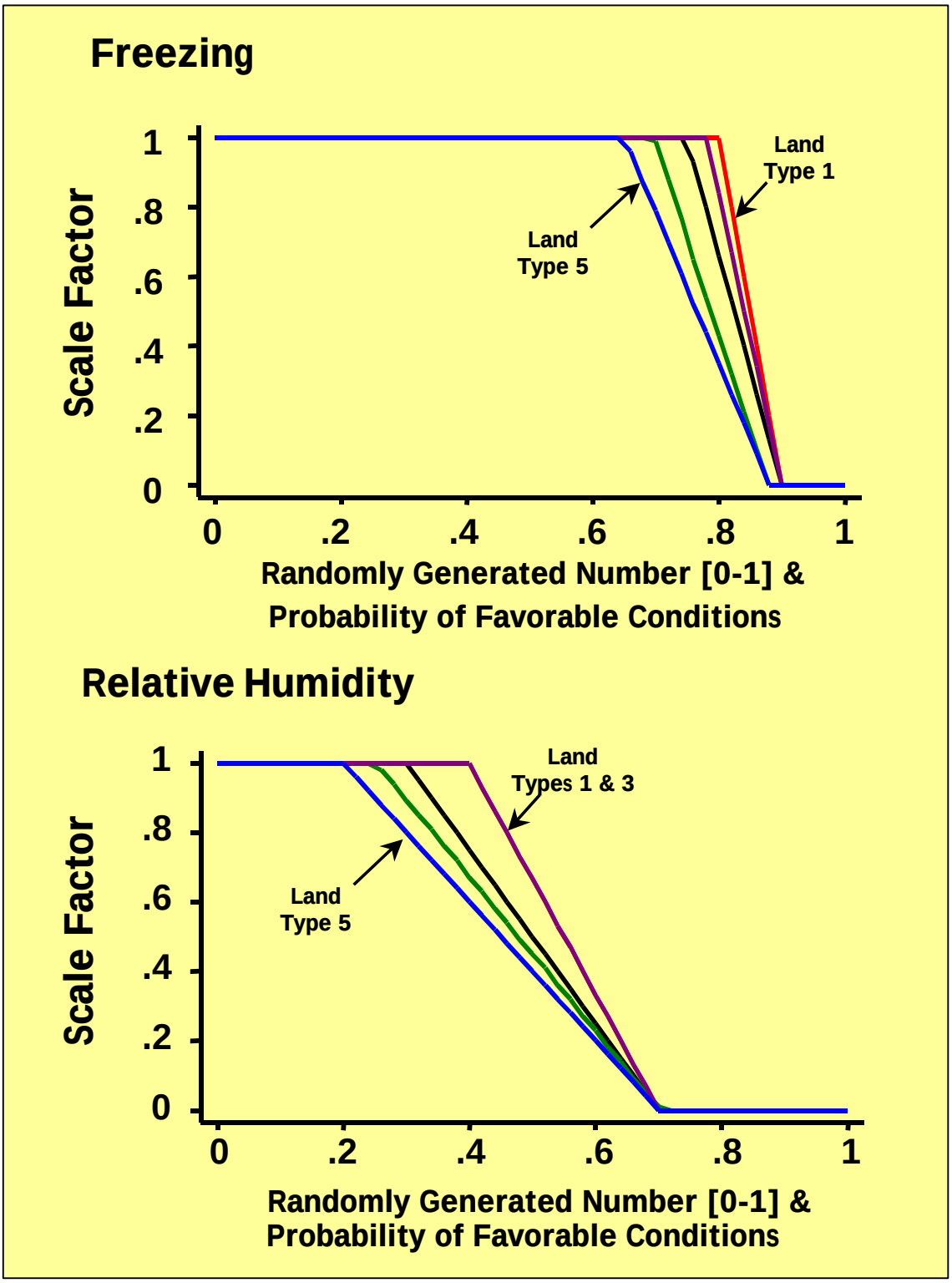

Figure IV.5 Influence of climate factors on mast index. A random number is generated and the influence of the factor (scale multiplier) is derived from the relationships shown.

mid-season failures in the model, although perhaps these flowers should be affected, although to a lesser extent.

IV.2.6 Model development: Previous mast production, scaling factors, and mast production

High levels of mast production in some years are thought to limit the amount of mast production in subsequent years either by limiting the resources available or through internal signals (Sork et al. 1993; Silvertown 1980). I accounted for this influence with the relationships shown in Figure IV.6. If the mast production scale factor for a given year is high, the scale factor for the next year is lowered. In the model, the mast production for the preceding two years affects current year mast production with the most recent year having the greatest influence. To model these differences, the red and white oak groups must be treated separately (Figure IV.1: Schematic references 6a, 6b, 6c). The red oak flower crop from the current year (t=n) is affected by the red oak scalars from the preceding two years (t=n-1 and t=n-2). This scale (t=n) value is then stored to be used in the next annual iteration as the acorn crop. The t=n-1 red oak scale (the previous year flower crop) is the current years mast scale factor and is multiplied by the potential mast production for red oaks (kg_ro) as generated in the spatial model (Figure IV1: Reference 7).

The influence of previous mast production on current-year white oak production is more direct since the current year flower crop is also the current year acorn crop. The influence of the previous production is factored (Steps 6a,b) and multiplied by the

potential white oak mast production generated by the spatial component of the mast model (kg_wo).

The total mast production is the sum of red and white oak production (Step 9 in Figure IV.1).

IV.3 MODEL PERFORMANCE

IV.3.1 Model performance: Introduction

The annual mast variability program module was applied to the output of the spatial mast model from the 90th year of the even-aged management scenario. I present the mean stand index (or kg ha^{-1}) as the basis for comparisons among years. The use of the 0-1 scaling factor in the annual model determines that mast production of the annual model cannot exceed mast production estimated in the spatial model. Therefore, the maximum amounts estimated in the spatial model are the potential mast production rates and the values estimated in the annual model are the estimated realized mast production after considering climate and other annually variable factors.

IV.3.2 Model performance: Annual variability

Figure IV.7 is a comparison of five independent simulations run on the same data set produced by the spatial mast model. Years of reasonably high mast production (about 300 kg ha^{-1}) usually occur in pairs with the second year often lower than the first. This is due to the differences in acorn development phenology between white and red oak

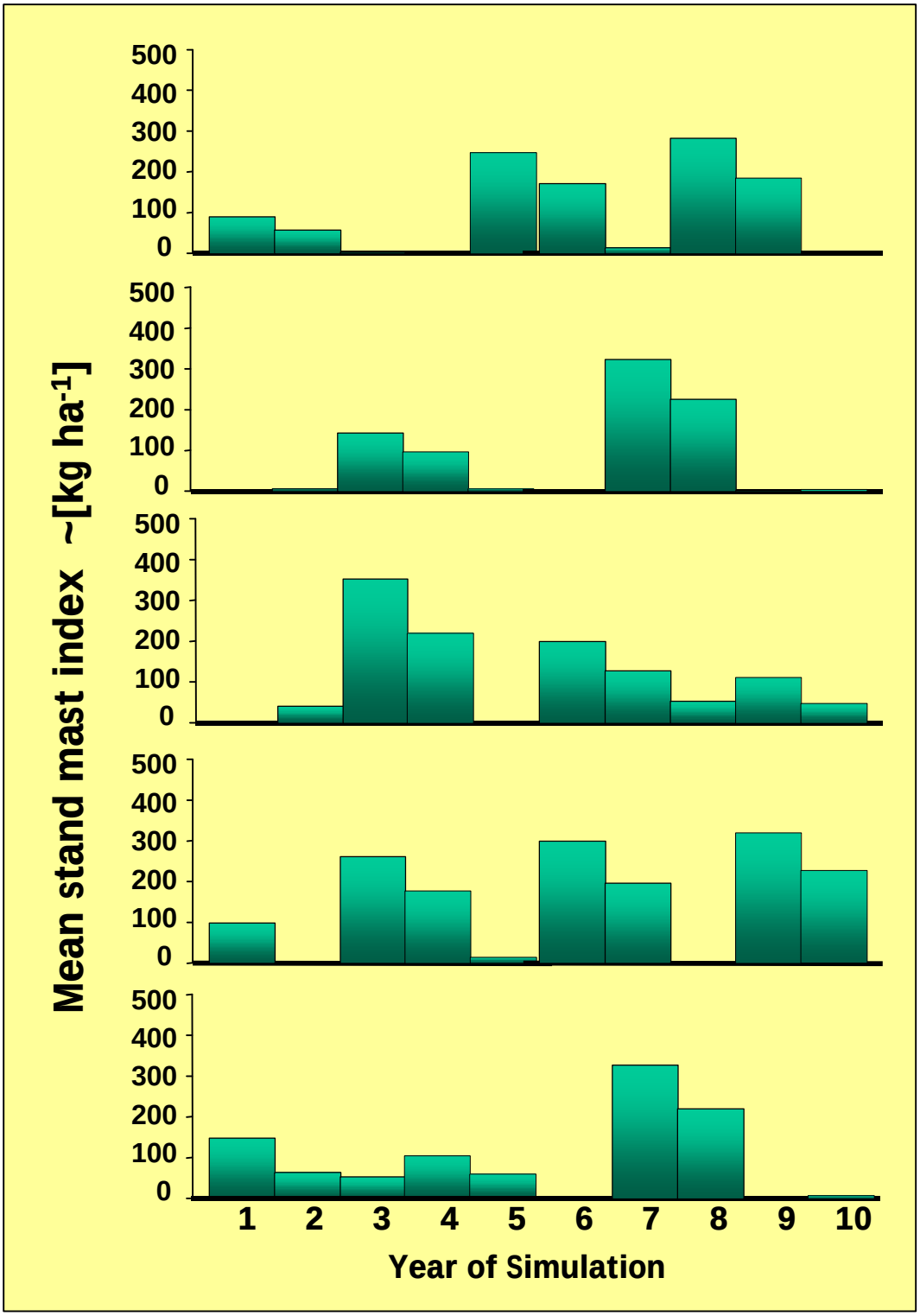

Figure IV.7 Five examples of 10-year model simulations adding annual variability to the 90th year output of the spatial MAST model. Values are the means across all stands in the landscape.

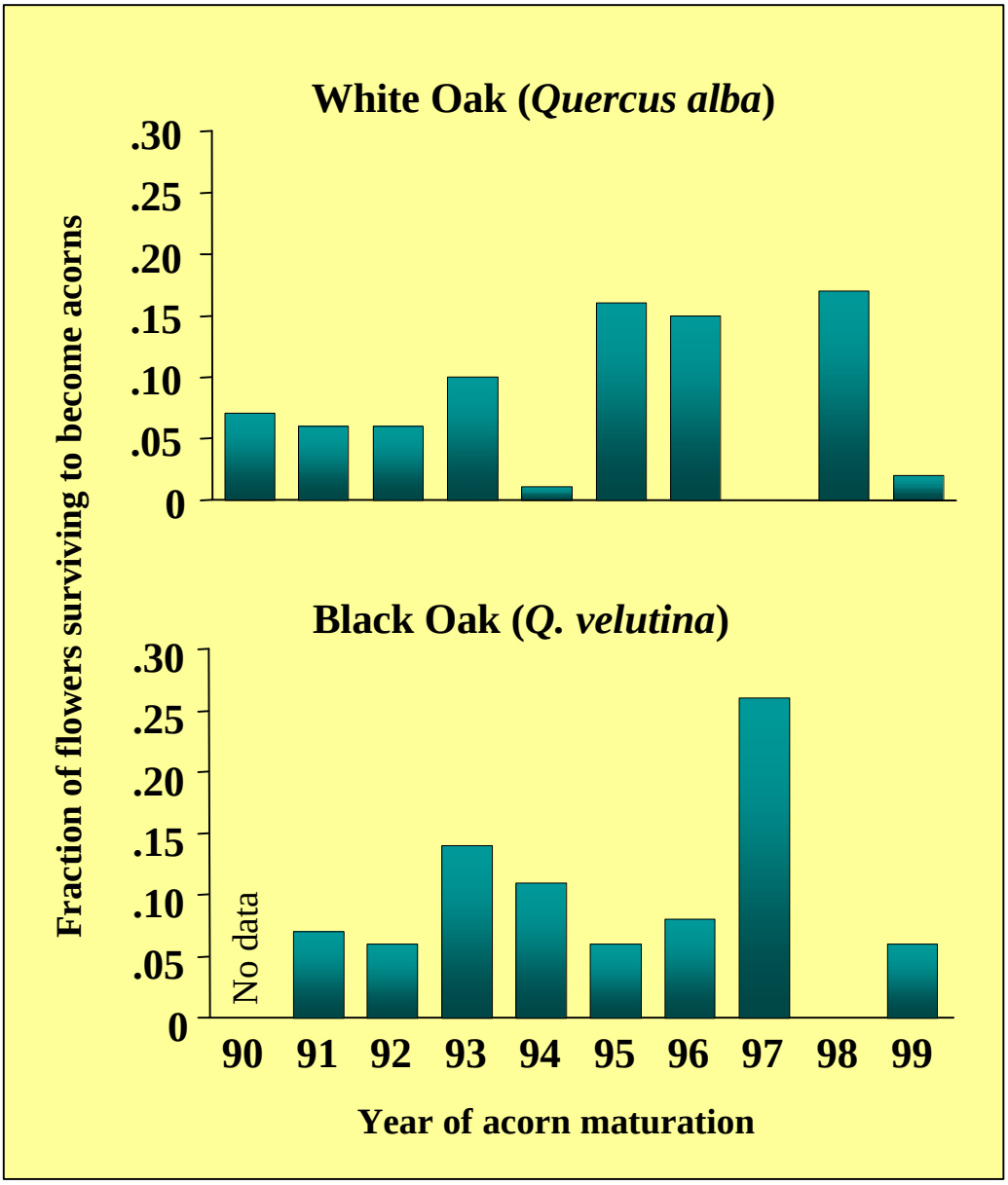

Figure IV.8 Variation in oak flower survival to become acorns among years for a study in central Missouri.. Production between species is offset due to reproduction phenology (Cecich and Sullivan, unpublished data).

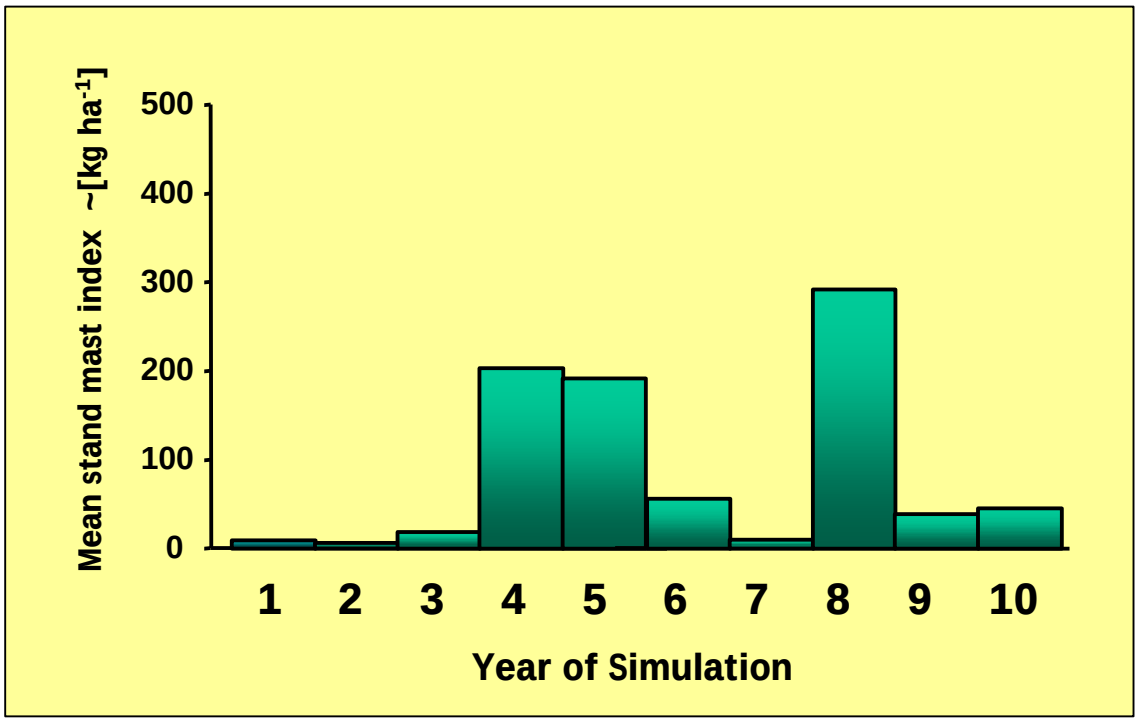

Figure IV.9 The mean stand mast index across all stands in the test landscape [or kg ha^{-1}] for a 10-year model simulation adding annual variability to the 90th year output This output is that used in the tables and maps depicting model specific behavior.

groups. When a good mast year occurs, the white oak crops are high that year and the red oak crops are high the second year. However, the white oak acorn crop for the second year will be lower since the previous high rate of mast production reduces stored resources. Hence, the acorn production the second year after the occurrence of favorable conditions for flowering is typically lower. The annual variability model does seem to predict a wide range of mast production rates, although, perhaps the occurrence of both very low crops and moderately high crops is too frequent. For the five 10-year simulations depicted in Figure IV.7, there was little or no mast production in eighteen of the 50 years shown (~22 per cent). Similarly, in a study of white and black oaks over 10 years in central Missouri, Cecich (1999) recorded little or no acorn production for three (30 %) of those years for the white oaks and for one (11 %) of the years for black oaks (Figure IV.8).

A log file for one simulation run was retained to examine the causes of mast crop failures. Table IV.4 lists the random numbers that were generated along with the scale factors associated with each number by land type. Also, the mature acorn production (mast crop) for that year is listed. For example in year 1, a year of very low mast production (Figure IV.9), the random numbers generated for both freezing temperatures and relative humidity (0.93 and 0.80, respectively) caused the scale factor to be 0 for flowers emerging that year. In year 3, the limiting factor in mast production was the warm-cool temperature regime factor (0.45). This factor reduces the white oak mast crop for that year and a relative humidity limitation in the previous year limits the red oak portion of the crop. Year 8 is the most productive year and nearly all of that production is from the white oak group. The good climate conditions that year (scalers = 1, 1, 0.54,

Table IV. 4 Scale factors and mast production for an example of a 10 tear simulation adding annual variability to the spatial mast model. Low T ifs for unfavorable spring freeze, RH = relative humidity, WC = warm-cool temperature regime , and Fail = Mid-season failure. WO and RO represent the red- and white- oak groups.

	Land Type	Low T	RH	WC	Fail	Mast WO	Mast RO	Mast Total
Year 0		---- *Random Number* ----				---- *kg ha*$^{-1}$ *or Index* ----		
		0.04	0.42	0.90	0.14	-	-	-
		---- *Scale Factor* ----						
	1	1.00	0.92	0.36	1.00			
	2	1.00	0.62					
	3	1.00	0.92					
	4	1.00	0.69					
	5	1.00	0.55					
	6	1.00	0.68					
	7	1.00	0.69					
Year 1		---- *Random Number* ----						
		0.93	0.80	0.70	0.64	0.00	0.00	0.00
		---- *Scale Factor* ----						
	1	0.00	0.00	0.52	1.00			
	2	0.00	0.00					
	3	0.00	0.00					
	4	0.00	0.00					
	5	0.00	0.00					
	6	0.00	0.00					
	7	0.00	0.00					
Year 2		---- *Random Number* ----						
		0.87	0.95	0.45	0.56	0.00	0.17	0.17
		---- *Scale Factor* ----						
	1	0.29	0.00	0.74	1.00			
	2	0.04	0.00					
	3	0.24	0.00					
	4	0.19	0.00					
	5	0.04	0.00					
	6	0.19	0.00					
	7	0.19	0.00					

	Land Type	Low T	RH	WC	Fail	WO	Mast RO	Total
Year 3		---- *Random Number* ----						
		0.12	0.68	0.79	0.60	18.10	0.00	18.10
		---- *Scale Factor* ----						
	1	1.00	0.06	0.45	1.00			
	2		0.05					
	3		0.06					
	4		0.05					
	5		0.04					
	6		0.06					
	7		0.04					
Year 4		---- *Random Number* ----						
		0.70	0.30	0.97	0.68	190.60	11.81	202.41
		---- *Scale Factor* ----						
	1	1.00	1.00	0.30	1.00			
	2	0.96	0.89					
	3	1.00	1.00					
	4	1.00	0.98					
	5	0.77	0.80					
	6	1.00	0.99					
	7	1.00	0.98					
Year 5		---- *Random Number* ----						
		0.001	0.03	0.31	0.11	59.60	124.90	184.50
		---- *Scale Factor* ----						
	1	1.00	1.00	0.85	1.00			
	2	1.00	1.00					
	3	1.00	1.00					
	4	1.00	1.00					
	5	1.00	1.00					
	6	1.00	1.00					
	7	1.00	1.00					

	Land Type	Low T	RH	WC	Fail	Mast Production WO	RO	Total
Year 6		---- *Random Number* ----						
		0.45	0.66	0.42	0.62	11.59	43.45	55.04
		---- *Scale Factor* ----						
	1	1.00	0.13	0.77	1.00			
	2	1.00	0.09					
	3	1.00	0.13					
	4	1.00	0.10					
	5	1.00	0.08					
	6	1.00	0.11					
	7	1.00	0.10					
Year 7		---- *Random Number* ----						
		0.01	0.79	0.81	0.06	0.00	7.39	7.39
		---- *Scale Factor* ----						
	1	1.00	0.00	0.43	1.00			
	2	1.00	0.00					
	3	1.00	0.00					
	4	1.00	0.00					
	5	1.00	0.00					
	6	1.00	0.00					
	7	1.00	0.00					
Year 8		---- *Random Number* ----						
		0.78	0.21	0.69	0.56	287.10	0.07	287.17
		---- *Scale Factor* ----						
	1	1.00	1.00	0.54	1.00			
	2	0.54	1.00					
	3	0.97	1.00					
	4	0.79	1.00					
	5	0.43	1.00					
	6	0.78	1.00					
	7	0.79	1.00					

	Land Type	Low T	RH	WC	Fail	Mast Production WO	RO	Total
Year 9		---- *Random Number* ----						
		0.09	0.14	0.67	0.87	0.05	36.25	36.30
		---- *Scale Factor* ----						
	1	1.00	1.00	0.55	0.20			
	2	1.00	1.00					
	3	1.00	1.00					
	4	1.00	1.00					
	5	1.00	1.00					
	6	1.00	1.00					
	7	1.00	1.00					
Year 10		---- *Random Number* ----						
		0.45	0.60	0.97	0.25	3.30	39.30	42.60
		---- *Scale Factor* ----						
	1	1.00	0.34	0.29	1.00			
	2	1.00	0.23					
	3	1.00	0.34					
	4	1.00	0.25					
	5	1.00	0.20					
	6	1.00	0.25					
	7	1.00	0.26					

and 1) are not reflected in the mast crop the following year because of the random assignment of a mast limiting mid-season failure event resulting in an 80 percent reduction in that crop.

IV.3.3 Model performance: Spatial variability

This example simulation is represented spatially in Figures IV.10 and IV.11. In Year 8, there is a set of stands represented by light shading scattered throughout the landscape (lower mast production), whereas in Year 5, all of the stands have dark shading indicating higher mast production. The relatively low production of some stands in Year 8 is due to the species distributions on those stands. The randomly assigned red oak fraction for these stands must be relatively high since nearly all of the mast production for that year comes from the white oak group (Table IV.4).

IV.4 CONCLUSIONS

The annual variability module for the spatial mast model estimates random variability based on the probability of favorable climate conditions for flowering success for any given year. An additional source of random variability was added in consideration of random climatic events (hail, drought *etc*.) and other random events (such as insect outbreaks). This random mid-season failure rate and the degree of damage to the mast crop will need to be more accurately quantified in later versions of this model. Also, the

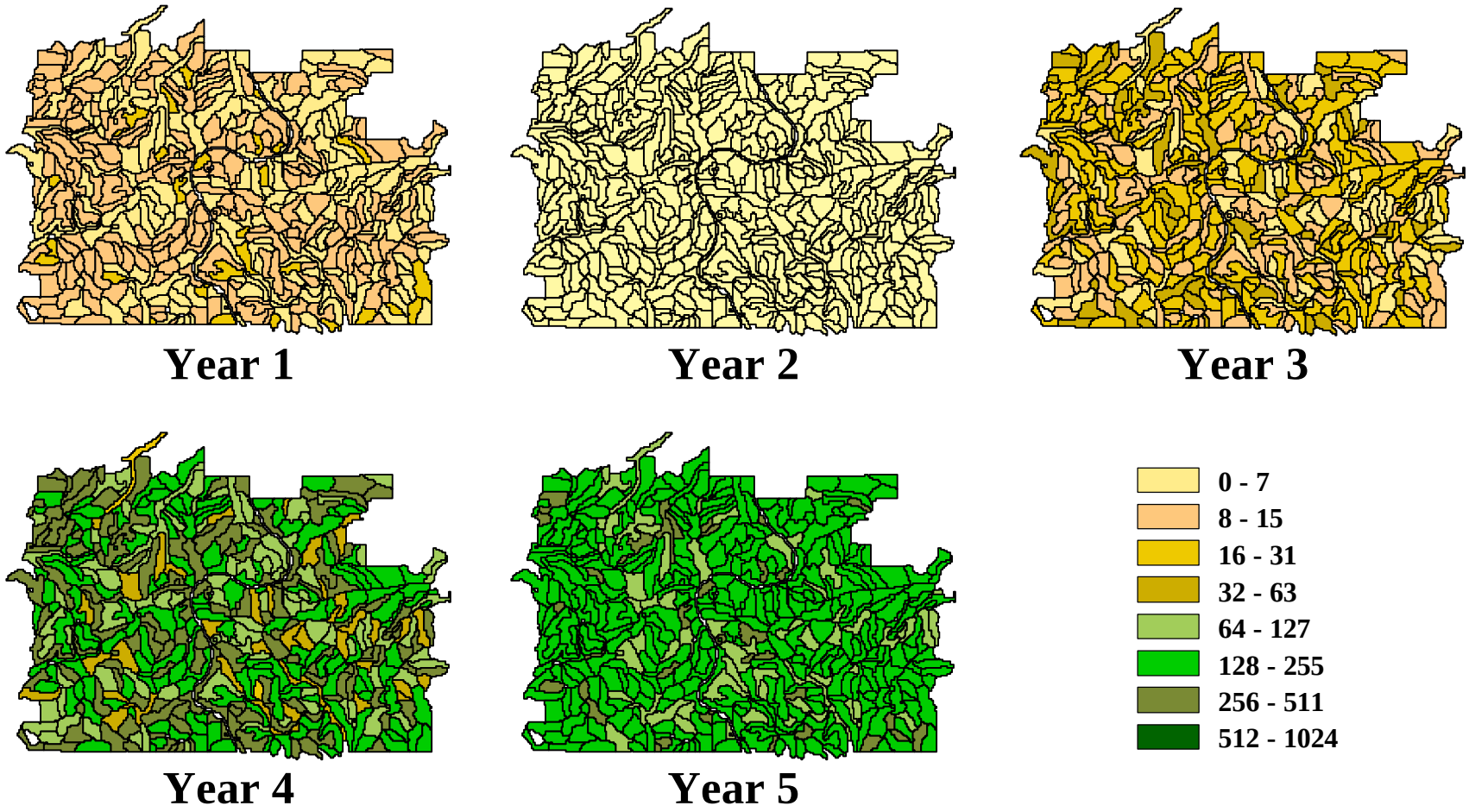

Figure IV.10 Mast production (index or kg ha^{-1}) for one simulation applying annual variability to one simulation of the spatial variability model applied to the Oregon County Landscape for the 90th year under even-aged management.

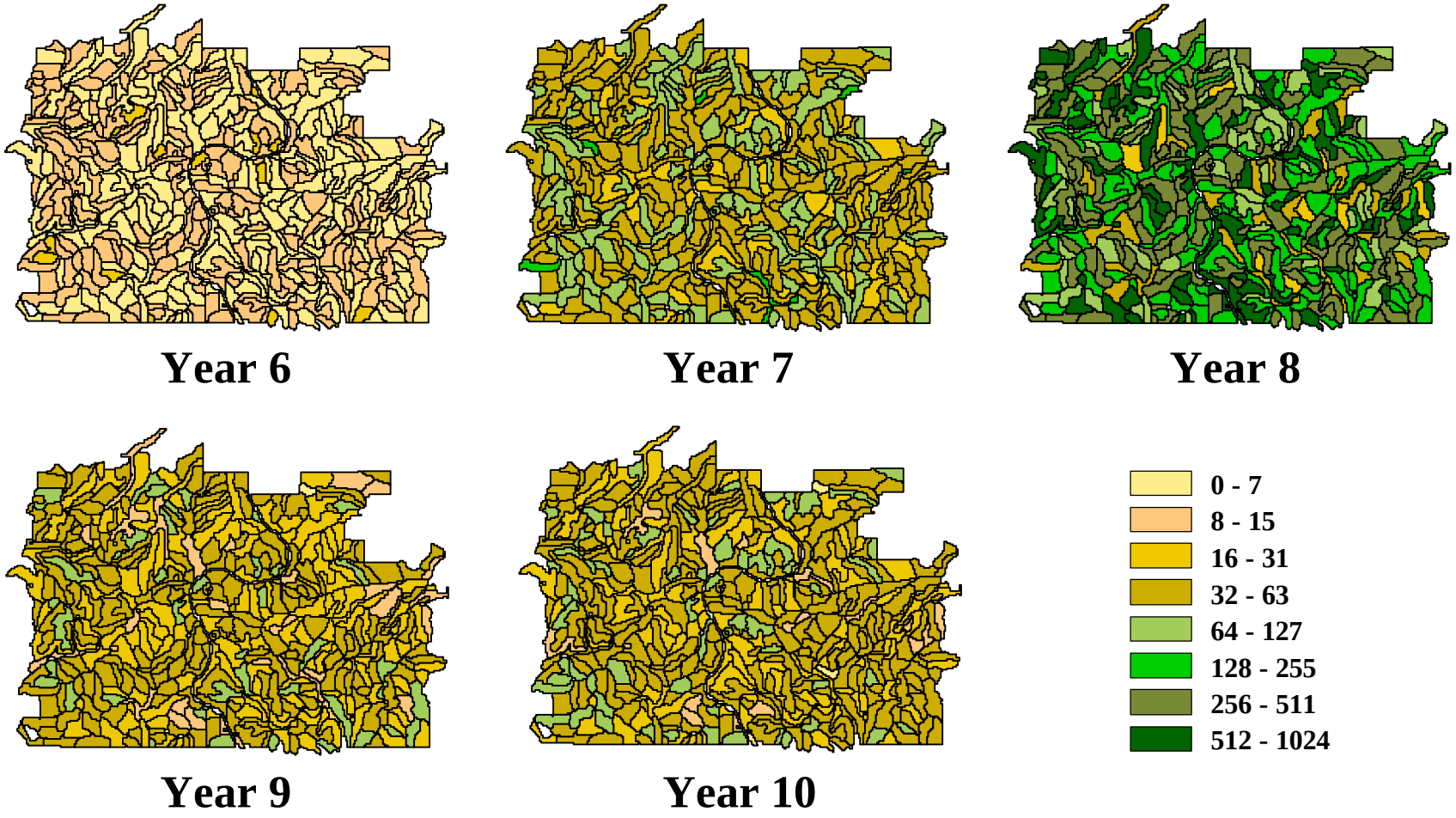

Figure IV.11 (continued) Mast production (index or kg ha^{-1}) for one simulation applying annual variability to one simulation of the spatial variability model applied to the Oregon County Landscape for the 90th year under even-aged management.

topographic variation in relative humidity and the influence of relative humidity needs to be better described. In general, previous research has shown that low relative humidity during flowering favors acorn production but the level of relative humidity and the gradients of masting response are not well described. In addition, there are three aspects of flowering success that may be influenced by relative humidity considerations, release of pollen, pollen dispersal, and the deposition of pollen on pistillate flowers. Pollen may be released at a location with low humidity, transported hundreds of miles by wind currents before potentially being deposited at a site with very different relative humidity conditions. Therefore, perhaps, both local and regional relative humidity levels are important.

Temperature and relative humidity are two components included in many models predicting global climate change. Relative humidity is both a driving factor (a "greenhouse gas") and a response factor (increasing RH due to increased evaporation arrising from temperature increases). In the concluding chapter of this dissertation (Section VI), I will present the results of a simulation run of the annual variability model under conditions of increased probability of freezing events and an increase in the occurrence of high relative humidity conditions.