SECTION V: ALLOCATION OF RESOURCES: THE TRADE-OFF BETWEEN VEGETATIVE GROWTH AND ACORN PRODUCTION

IV.1 INTRODUCTION

During the 1999 growing season, along with the 10th annual observation of flower production and survival of *Quercus alba* and *Q. velutina* trees at the Baskett Research area in Ashland, Missouri, we measured the change in diameter occurring across the season on the individual branches where flower development was observed. In addition, at the beginning of the growing season, we collected branches from each of those trees to examine previous branch growth increment to compare to their 10-year tree-level mast production history. This section presents the findings of that study as they relate to masting.

Due to suspected global climate change and the role that carbon plays as a component of carbon-dioxide (a greenhouse gas) as well as interest in the storage of carbon, a large amount of research on the carbon cycle has been conducted recently (*e.g*. Vogt 1991; Valentine *et al*. 1997; Makela 1997; Bartelink 1998). In general, the allocation of resources to reproduction is ignored in stand-to-landscape level models because it represents a relatively small part of the total carbon budgets of these systems. For example, Vogt (1991) presented data describing typical carbon budgets for several forest types and estimated that the biomass (weight) for the foliar component of a mixed-hardwood forest is about 4,700 kg ha^{-1}. The highest mast production rates in the literature range from 400 to 1500 kg ha^{-1} or about 9 to 30 percent of the foliar weight. However, the foliar component of the forest is a net-fixer (importer) of energy for a tree whereas reproductive structures are a net energy expense. Merely partitioning forest biomass among components does not adequately describe the system. Reekie and Bazzaz (1987), after studying resource allocation in *Agropyron repens* concluded that a significant amount resources were involved with reproduction, but that the costs could not be described completely by simply measuring reproductive structures. Respiratory costs, lower resource availability for photosynthetic tissues, the photosynthetic contribution of the reproductive tissues themselves, increased stem tissue to support reproductive tissues should all be considered.

Norton (1988), in a study of a frequently masting podocarp tree, Rimu (*Dacrydium cupressinum* Lamb.), found that radial growth during masting years was less than that of non-masting years, suggesting a shift in allocation from vegetative to reproductive structures. Sork *et al*. (1993) in a study of oak masting in Missouri, found that previous acorn crops had an impact on the current year acorn crop, suggesting that masting alters allocation patterns in oak. Seki (1994) reported that the amount carbohydrate storage adjacent (stem and branch) to fruiting branch segments influenced the number of cones produced in fir (*Abies mariesii*). Waring and Schlesinger (1985) reported that allocation of resources to pine cones could reduce vegetative growth but that stressful environmental conditions could also alter allocation patterns. Although viewing allocation from a different perspective (nut production), Malstrom and McMeans (1982) found that pecan [*Carya illinoensis* (Wang) K.Koch] shoots that produced fruit one year would have shorter growth the next-year than shoots that were strictly vegetative.

In this section, I review the results of two aspects of branch measurements made in 1999: i) *in situ* measurements of radial growth of branch ends monitored for flower and acorn production, ii) modified stem analysis of branches to evaluate the impact of mast production on radial and shoot-length growth over 10 years.

V.2 METHODS

V.1.1 Methods: Mast production index

From 1991 to 1999, beginning in mid- to late-April Oak flowers were counted and monitored for viability at critical stages of development on 5 branch-ends for each of nine white oaks and twelve black oaks (Cecich and Sullivan 1999). All sample trees were over 20 m in height ranging in diameter (dbh) from 17 to 63 cm, occupied either dominant or co-dominant canopy positions, and all branches received full sunlight. These measurements were conducted using a truck equipped with a hydraulic boom enabling us to reach the upper canopy (approximately 19 m in height) of these roadside trees.   During this period, a considerable amount of variation in mast production was recorded among trees and among years (Figure V.1; Table V.1). An index to productivity by species for each tree and each year was generated by dividing the number of acorns produced each year for each tree by the maximum number of acorns produced for <u>any</u> year (Table V.2). The maximum production rate over this period for these trees is not known, however, this index provides a relative index of performance among trees and among years.   The index for each year by tree was compared to the corresponding mast production.

Table V.1. Among year and among tree variation in the number of acorns produced from 5 branch ends from each of 21 trees.

	Tree No.	90	91	92	93	94	95	96	97	98	99	*Total*	*Average*	*SD*
		Year of Acorn Maturation (Primary C Allocation)												
Quercus alba	**1**	6	4	0	0	0	6	4	0	14	0	34	3.40	4.53
	2	5	15	4	8	0	8	9	0	14	4	67	6.70	5.14
	3	4	3	1	0	0	0	0	0	0	0	8	0.80	1.48
	4	0	0	1	0	0	11	0	0	2	0	14	1.40	3.44
	6	8	3	5	6	3	16	4	0	25	0	70	7.00	7.82
	7	0	1	0	2	0	9	1	0	2	0	15	1.50	2.76
	8	1	1	0	4	0	32	6	0	4	0	48	4.80	9.80
	9	6	0	1	1	0	6	3	0	0	1	18	1.80	2.39
	11	62	0	9	13	0	15	23	0	46	0	168	16.80	21.45
		9	9	9	9	9	9	9	9	9	9			
	Total	92	27	21	34	3	103	50	0	107	5	442		
	Average	10.22	3.00	2.33	3.78	0.33	11.44	5.56	0.00	11.89	0.56		4.91	
	SD	19.63	4.74	3.08	4.49	1.00	9.11	7.16	0.00	15.35	1.33			9.62
Q. velutina	**1**		2	0	11	17	4	2	19	0	9	64	7.11	7.25
	2		10	0	21	8	0	3	21	0	0	63	7.00	8.76
	3		0	11	2	14	12	9	3	0	0	51	5.67	5.77
	4		14	0	1	3	0	3	12	0	1	34	3.78	5.38
	5		0	0	0	1	0	0	0	0	1	2	0.22	0.44
	6		9	0	6	7	0	1	8	0	0	31	3.44	3.94
	7		0	0	0	5	6	0	0	0	11	22	2.44	4.00
	8		1	12	15	2	5	7	18	0	3	63	7.00	6.52
	9		3	0	4	4	0	5	20	0	2	38	4.22	6.22
	10		22	4	24	0	8	9	15	0	1	83	9.22	9.23
	11		49	25	19	18	1	12	19	0	2	145	16.11	15.35
	12		0	0	0	0	0	0	0	0	0	0	0.00	0.00
	Total		110	52	103	79	36	51	135	0	30	596		
	Average		9.17	4.33	8.58	6.58	3.00	4.25	11.25	0.00	2.50		5.52	
	SD		14.36	7.87	9.03	6.44	4.02	4.11	8.58	0.00	3.66			8.03

	90	91	92	93	94	95	96	97	98	99
Qa mean	10.22	3.00	2.33	3.78	0.33	11.44	5.56	0.00	11.89	0.56
se	6.54	1.58	1.03	1.50	0.33	3.04	2.39	0.00	5.12	0.44
Qv mean		9.17	4.33	8.58	6.58	3.00	4.25	11.25	0.00	2.50
se		4.14	2.27	2.61	1.86	1.16	1.19	2.48	0.00	1.06

Table V.2 . Among year and among tree variation in the number of acorns produced from 5 branch ends from each of 21 trees expressed as an index from 0 - 100 where 100 is the maximum number of acorns produced by any tree by species across all years.

		Year of Acorn Maturation (Primary C Allocation)										
	Tree No.	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	***Average***
Quercus alba	**1**	10	6	0	0	0	10	6	0	23	0	5
	2	8	24	6	13	0	13	15	0	23	6	11
	3	6	5	2	0	0	0	0	0	0	0	1
	4	0	0	2	0	0	18	0	0	3	0	2
	6	13	5	8	10	5	26	6	0	40	0	11
	7	0	2	0	3	0	15	2	0	3	0	2
	8	2	2	0	6	0	52	10	0	6	0	8
	9	10	0	2	2	0	10	5	0	0	2	3
	11	100	0	15	21	0	24	37	0	74	0	27
	Average	16	5	4	6	1	18	9	0	19	1	8
Q. velutina	**1**		4	0	22	35	8	4	39	0	18	15
	2		20	0	43	16	0	6	43	0	0	14
	3		0	22	4	29	24	18	6	0	0	12
	4		29	0	2	6	0	6	24	0	2	8
	5		0	0	0	2	0	0	0	0	2	0
	6		18	0	12	14	0	2	16	0	0	7
	7		0	0	0	10	12	0	0	0	22	5
	8		2	24	31	4	10	14	37	0	6	14
	9		6	0	8	8	0	10	41	0	4	9
	10		45	8	49	0	16	18	31	0	2	19
	11		100	51	39	37	2	24	39	0	4	33
	12		0	0	0	0	0	0	0	0	0	0
	Average		19	9	18	13	6	9	23	0	5	11

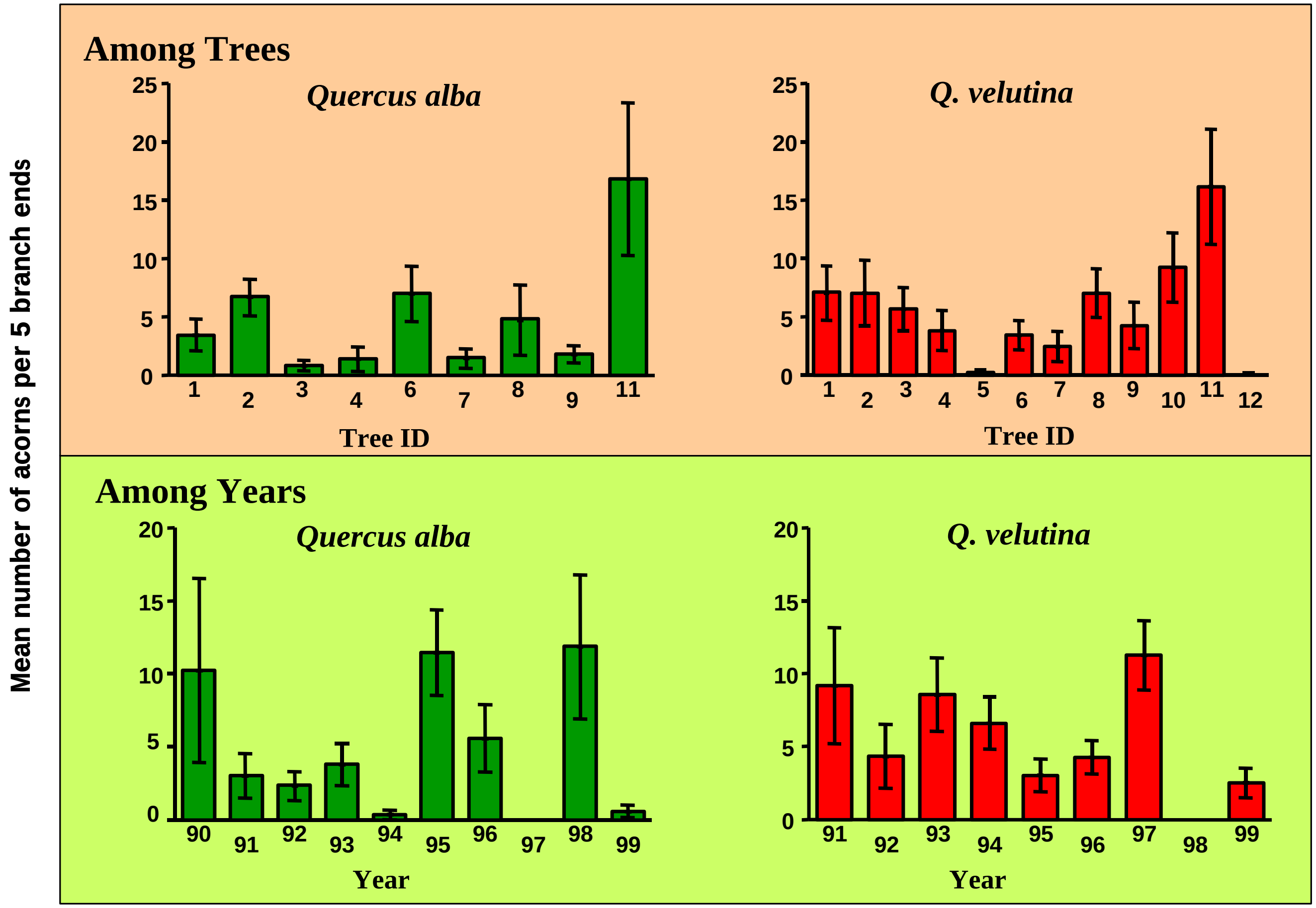

Figure V.1 Variation in acorn production among trees and among years for 5 branch ends from 21 trees in central Missouri.

V.1.1 Methods: In situ diameter measurements

In 1999, one week after the initial selection of shoots for monitoring flower development, the diameter of each shoot was measured at a point on the shoot that accommodated the instrument (a mechanical digital-micrometer with a resolution of 0.0254 mm). The shoot was labeled at the point of measurement in a manner that indicated the orientation of the instrument to ensure future measurements were made along the same radius. Re-measurements were made periodically throughout the growing season and at the end of the growing season.

Since the point of measurement for each branch differed in distance from the shoot tip, the change in diameter across the entire season was expressed as the percentage increase in cross-sectional area.

V.1.1 Methods: Ex situ historical branch measurements

On June 21st, 1999, one branch from each tree was excised at a point distal to the shoot tips adequate to ensure at least 10 years of growth (usually 3-4 cm in diameter at the base). In the lab, branches were sectioned to produce 3 or 4 manageable units. Leaves were removed leaving the petiole, three transverse cross-section samples were taken, and the following procedure was used to record growth:

1. Each branch was mapped starting at the shoot tips and working as far backward as year-of-growth could be determined by examining the outer bark. Annual shoot growth was indicated by scarring aound the circumference of branches.

2. Beginning at the oldest identifiably complete branch section, the length and diameter (distal to the tip but not affected by swelling a the yearly juncture) was measured working toward the shoot-tip. Length was measured to the nearest cm and diameter to 0.025 mm.

3. Notations were recorded that included: i) the size and location of any damage to the outer bark (1997 was a year periodic cicada emergence), ii) the number of developing acorns from 1998 flowers (*Q. velutina*) and 1999 flowers (*Q. alba*), iii) the number of "dormant" 1999 flowers (*Q. velutina*), iv) and the number of leaves.

In addition to outside radial measurements, the ring widths were measured from the cross-sections sampled at the base of each branch section using an optical-digital measuring device (R. Guyette, pers. comm.).

V.3 RESULTS AND DISCUSSION

V.3.1 Results and discussion: In situ branch measurements

The *Q. velutina* trees were more variable in terms of the percentage change in cross section and in the number of acorns produced (Table V.3). Indeed, one *Q. velutina* tree (No. 7) appeared to decrease in diameter. Due to measurement error and the effects of shrinkage from late-season water shortages, many measurements at the end of the season were lower than the initial measurement. However, the measurements for all five shoots were lower on tree 7. Notably, this tree had one of the highest average acorn

Table V.3 Summary of 1999 *in situ* branch measurements

Tree ID	Tree Diameter DBH [cm]	Average Mast Index Value[1]	N	Cross Sectional Area [mm²] Initial Mean SD	Ending Mean SD	Percent Change Mean SD	Number of Leaves Mean SD	Number of Flowers Mean SD	Number of Acorns Mean SD
Quercus alba									
2	41	11	5	22.4 *(11.8)*	25.1 *(12.8)*	13.4 *(13.1)*	23 *(7)*	6 *(3)*	0.8 *(0.84)*
4	48	2	5	20.1 *(7.0)*	22.8 *(5.6)*	16.6 *(15.4)*	31 *(17)*	12 *(5)*	0
7	63	2	5	15.1 *(1.3)*	19.7 *(1.6)*	31.4 *(12.7)*	26 *(4)*	9 *(4)*	0
8	53	8	5	11 *(3.3)*	12.1 *(3.8)*	9.6 *(11.8)*	23 *(6)*	6 *(3)*	0
9	50	3	5	18.9 *(4.6)*	22.7 *(7.2)*	19 *(11.9)*	28 *(10)*	11 *(5)*	0.2 *(0.45)*
Quercus velutina									
1	32	15	8	22.1 *(11.4)*	23.9 *(11.1)*	14.1 *(27.6)*	19 *(11)*	7 *(4)*	3 *(5.2)*
2	39	14	5	26.4 *(7.5)*	27.7 *(7.5)*	5 *(2.2)*	21 *(7)*	4 *(4)*	0
3	43	12	5	24.1 *(7.8)*	26.9 *(8.6)*	11.9 *(4.7)*	20 *(6)*	5 *(2)*	0
4	34	8	7	22.3 *(8.2)*	23.6 *(6)*	16.6 *(22.3)*	15 *(12)*	4 *(4)*	0.5 *(0.71)*
5	36	0	10	31.5 *(28.8)*	35.5 *(31.6)*	13.1 *(14.6)*	14 *(7)*	7 *(1)*	0.2 *(0.45)*
6	17	7	4	11.1 *(1.1)*	12.5 *(1.7)*	13.6 *(15.4)*	6 *(2)*	0	0
7	35	5	9	20.7 *(9.3)*	25.6 *(7.4)*	-9.6 *(6.1)*	13 *(8)*	1 *(2)*	2.75 *(0.5)*
8	35	14	9	26.2 *(14.3)*	27.7 *(14.9)*	7.7 *(8.9)*	12 *(8)*	2 *(2)*	0.75 *(0.5)*
9	25	9	7	22.5 *(13.2)*	24.1 *(11.9)*	11.6 *(15.5)*	15 *(10)*	6 *(3)*	1 *(1.41)*
10	31	19	7	18.5 *(5.4)*	21.1 *(7.1)*	14.1 *(16.7)*	17 *(10)*	6 *(1)*	0.5 *(0.71)*
11	30	33	8	22.3 *(6.1)*	24.3 *(7)*	8.8 *(7.7)*	22 *(18)*	10 *(6)*	0.67 *(1.15)*
12	31	0	8	27.9 *(15.7)*	39.9 *(30)*	36.8 *(31.1)*	21 *(10)*	8 *(3)*	0

1. Mast index value is the number of acorns produced per 5 branch ends divided by the maximum number of acorns produced for all trees and all years by species

production rates with 2.75 acorns per shoot but one of the lower mast indices (5). Otherwise, for *Q. velutina* the difference in cross-sectional growth ranged from around 5 percent to over 35 percent with a slightly narrower range for *Q. alba.*

Insufficient data were available for analysis of the influence of masting on branch growth by species. However, when factoring both species, acorn production had a significant negative influence on the change in cross-sectional area (Figure V.2) using simple linear regression and robust regression techniques (to reduce the influence of outliers). That is, more acorns corresponded to lower diameter growth in 1999.

V.3.2 Results: Ex situ measurements of branch growth.

Due to the manner of sampling, the number of measurements by year ranged from about 1150 for the 1999 shoots (branch ends) to about 30 branch segments in 1992. For some branch sections it was not possible to accurately determine the year of growth; therefore, branch length growth measurements may only reach as far in the past as 1994 (Table V.4) and varied among branches in the number of years measured. Since many factors can influence both shoot growth and acorn production (e.g. inherent genetic factors, drought, insect outbreaks, hail etc), discerning significant relationships would require a much more extensive or intensive data set. A more extensive data set would include measurements similar to those made in this study but upon a much larger number of trees, a more intensive data set would track growth and acorn production for specific branches across many years. As it is, I only have one index value for each tree and for each year and this severely limits analyses.

Table V.4 Summary statistics for branch length growth for Baskett area oak tree branch analysis (modified stem analysis).

	Tree ID	Year	N	Branch length Growth [cm] Mean	SD	Min	Max
Quercus alba	1	91	2	5.00	0.00	5	5
	1	92	4	4.50	2.27	2	7.5
	1	93	7	2.79	0.91	2	4
	1	94	8	6.13	1.66	4	8.5
	1	95	10	6.25	1.34	4.5	8.5
	1	96	13	6.08	2.41	3.5	11
	1	97	20	5.70	2.33	2	9.5
	1	98	63	4.23	1.71	1.5	9
	1	99	109	3.26	2.02	0.5	11.5
	2	91	0				
	2	92	0				
	2	93	1	16.00	.	16	16
	2	94	2	16.83	0.45	16.51	17.15
	2	95	8	8.19	4.15	3.81	13.97
	2	96	13	8.67	4.33	3.05	18.03
	2	97	23	5.71	3.75	1.02	14.48
	2	98	56	6.59	3.81	1.91	18.29
	2	99	137	4.56	3.53	0	23.4
	4	91	0				
	4	92	0				
	4	93	2	10.50	3.54	8	13
	4	94	2	14.75	8.13	9	20.5
	4	95	11	10.36	4.92	5	18
	4	96	22	5.86	3.16	2	14
	4	97	32	3.13	2.00	0.5	9.5
	4	98	58	4.04	2.48	0.25	12.5
	4	99	99	3.50	2.62	0.3	13.5
	6	91	0				
	6	92	0				
	6	93	1	12.00	.	12	12
	6	94	4	8.50	1.91	7	11
	6	95	6	11.75	4.70	7	20.5
	6	96	14	9.25	4.08	4.5	19
	6	97	33	5.02	2.47	1.5	11
	6	98	51	5.02	3.09	2	16
	6	99	108	4.01	2.04	1	11

Tree ID	Year	N	Mean	SD	Min	Max
7	91	1	2.50	.	2.5	2.5
7	92	2	6.00	5.66	2	10
7	93	4	8.00	2.86	4	10.5
7	94	7	7.43	4.26	2	14
7	95	9	4.61	1.75	2	7
7	96	12	6.33	2.68	2.5	10
7	97	17	3.21	1.99	1	8
7	98	36	5.43	2.86	2	12.5
7	99	69	2.78	1.54	1	7
8	91	0				
8	92	3	14.00	1.73	12	15
8	93	3	7.67	3.79	5	12
8	94	5	7.80	3.68	4	13
8	95	10	8.25	1.55	5.5	10.5
8	96	11	7.68	2.03	5	11
8	97	23	5.54	1.77	2.5	9
8	98	56	5.61	1.98	2	10
8	99	118	3.27	1.62	1	8.5
9	91	0				
9	92	0				
9	93	0				
9	94	1	17.00	.	17	17
9	95	4	11.13	1.44	10	13
9	96	7	10.07	2.05	8	13.5
9	97	12	6.08	2.84	3	11.5
9	98	28	8.13	3.38	3	15
9	99	68	4.76	1.77	1.5	10.5
11	91	0				
11	92	2	7.25	3.89	4.5	10
11	93	2	3.50	2.12	2	5
11	94	3	7.17	1.26	6	8.5
11	95	4	7.13	0.85	6	8
11	96	7	9.36	3.61	3	13
11	97	13	5.46	3.18	1.5	11.5
11	98	21	5.19	2.91	1.5	11
11	99	31	4.11	2.25	1.5	11
	Overall Mean		7.06	2.69	4.13	11.91

	Tree ID	Year	N	Mean	SD	Min	Max
Quercus velutina							
	1	91	0				
	1	92	0				
	1	93	0				
	1	94	3	28.00	3.46	26	32
	1	95	7	10.93	4.54	6.5	18.5
	1	96	12	17.75	8.13	7	28
	1	97	20	7.68	9.40	1.5	28
	1	98	38	9.04	4.88	1	20
	1	99	54	7.29	3.19	2.5	21.5
	2	91	1	8.00	.	8	8
	2	92	4	8.75	0.96	8	10
	2	93	5	7.30	1.92	5	9
	2	94	8	11.31	6.17	3	20
	2	95	10	6.85	4.42	1	13
	2	96	13	4.85	2.65	1.5	11
	2	97	17	3.85	2.60	2	12.5
	2	98	21	3.24	2.14	1	9
	2	99	26	2.90	1.24	1	6
	6	91	2	8.75	0.35	8.5	9
	6	92	4	7.88	3.33	3	10
	6	93	6	11.42	4.91	5.5	17.5
	6	94	14	25.69	16.30	0	53
	6	95	29	5.79	2.33	1.8	10
	6	96	30	6.64	4.42	2	15
	6	97	52	5.47	3.71	1.5	17
	6	98	52	5.80	4.57	1	20
	6	99	65	5.43	5.05	0.5	21
	7	91	0				
	7	92	2	5.50	0.00	5.5	5.5
	7	93	3	10.00	5.20	4	13
	7	94	3	14.50	6.06	7.5	18
	7	95	6	8.72	3.78	4.8	16
	7	96	11	14.18	13.02	2.5	43
	7	97	22	8.37	10.12	1.8	40
	7	98	39	11.08	6.05	2.5	22
	7	99	50	4.56	2.99	0.5	14.5

Tree ID	Year	N	Mean	SD	Min	Max
8	91	0				
8	92	2	12.50	7.78	7	18
8	93	3	13.67	4.44	8.8	17.5
8	94	5	12.70	2.45	9.5	15.5
8	95	6	10.97	3.70	5.2	15
8	96	10	9.94	4.07	5	15
8	97	16	7.86	3.95	1	15
8	98	24	8.31	4.48	1.4	17.3
8	99	41	5.94	2.72	2	12.7
9	93	0				
9	94	1	16.00	.	16	16
9	95	4	19.63	3.20	17	24
9	96	6	11.27	6.77	2.7	18.7
9	97	11	14.35	11.81	1.4	38
9	98	21	9.53	5.56	2.5	22
9	99	31	4.75	2.60	1	10.5
10	93	0				
10	94	1	27.00	.	27	27
10	95	4	8.13	2.95	4	10.5
10	96	4	19.38	15.01	4	32.5
10	97	7	13.93	9.74	2	31
10	98	13	7.92	3.67	3.5	16
10	99	21	11.27	8.03	2	38
11	92	0				
11	93	2	8.50	0.00	8.5	8.5
11	94	17	20.82	8.78	2	33
11	95	12	6.83	1.50	5	9
11	96	21	12.19	5.26	2	20
11	97	30	8.20	7.82	1	24
11	98	73	7.37	4.44	1.5	18
11	99	93	4.57	2.23	0	10
12	91	0				
12	92	0				
12	93	0				
12	94	1	17.00	.	17	17
12	95	2	10.75	6.01	6.5	15
12	96	5	13.10	9.09	2	21.5
12	97	7	8.00	5.74	1	19.5
12	98	18	11.78	6.79	2	25
12	99	27	5.78	4.77	1.5	20
	Overall Mean		10.42	5.13	4.63	19.10

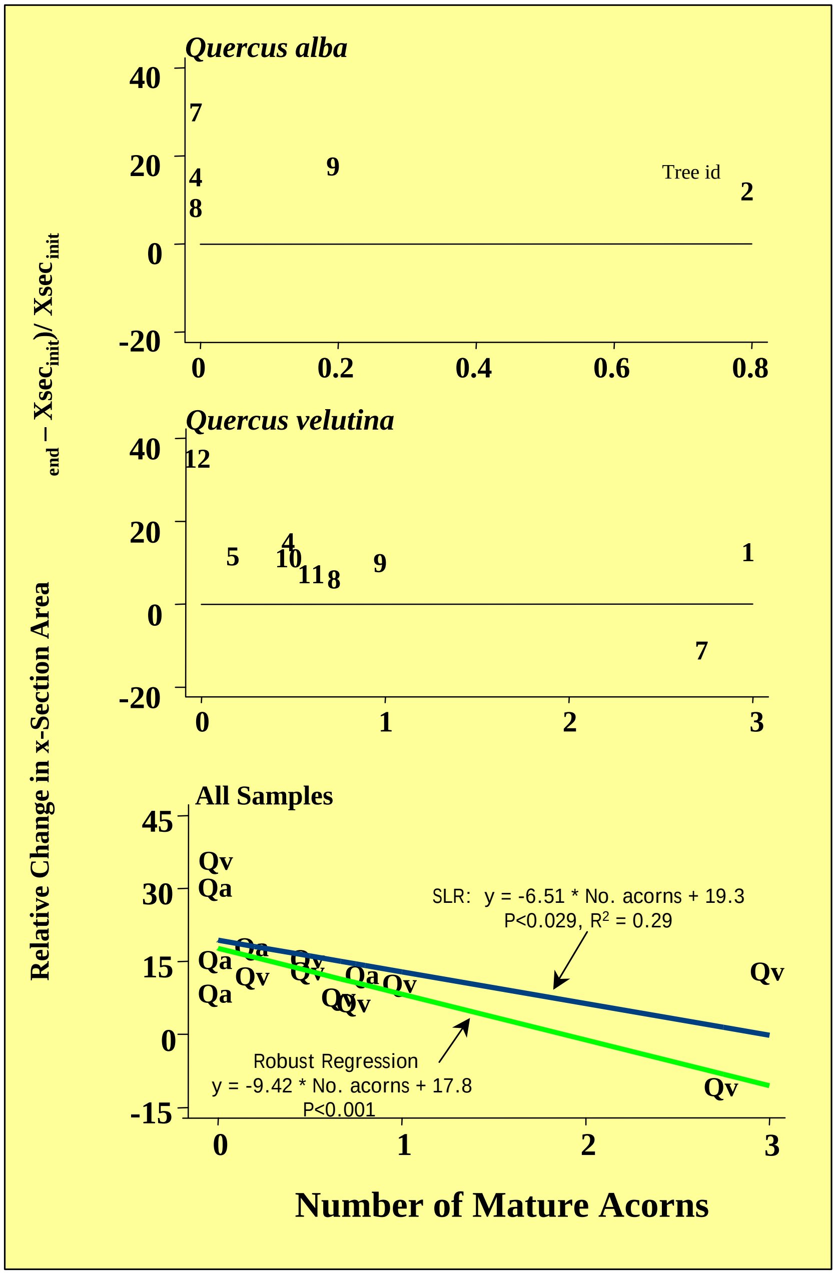

Figure V.2 The relationship between the number of maturing acorns and the relative change in cross-sectional area for 14 oak trees during the 1999 growing season.

Since I believe that one of the controlling factors for mast production is general tree health or vigor, I have divided the trees into three groups: trees that are generally high, moderate, or low mast producers. Trees that are generally good mast producers might be presumed to be more healthy, thus more able to store energy for future mast production and vegetative growth regardless of environmental conditions. Trees that are low mast producers may be more susceptible to environmental stress and apt to respond to those stresses.

V.3.3 Results: Ex situ measurements of branch growth: Shoot length

Two measurements of branch growth were recorded: diameter and shoot length. Diameter growth occurs throughout the growing season, although the rate of growth declines later in the season. Therefore, diameter measurements could be influenced by a combination of environmental stress and allocation of resources to acorn growth. Shoot growth for mature oaks begins and ends only in the spring prior to leaf-out and flowering. Thus, shoot growth is most influenced by environmental conditions only during this shorter growth period. Shoot length growth is dependent upon stored energy and the amount of available stored energy may be influenced by environmental conditions the previous year. These conditions include: moisture availability, temperature regime, light during the season, biotic stressors (predation), and perhaps allocation of resources to masting. Figures V.3 and V.4 show the relative branch length growth (measurement – mean per tree) for the three productivity groups. In the figures the plotted shoot length corresponds to the year of growth. For the mast index, it is the index for the tree for the year of acorn maturation for the year prior to shoot growth. For example, in 1997, a late

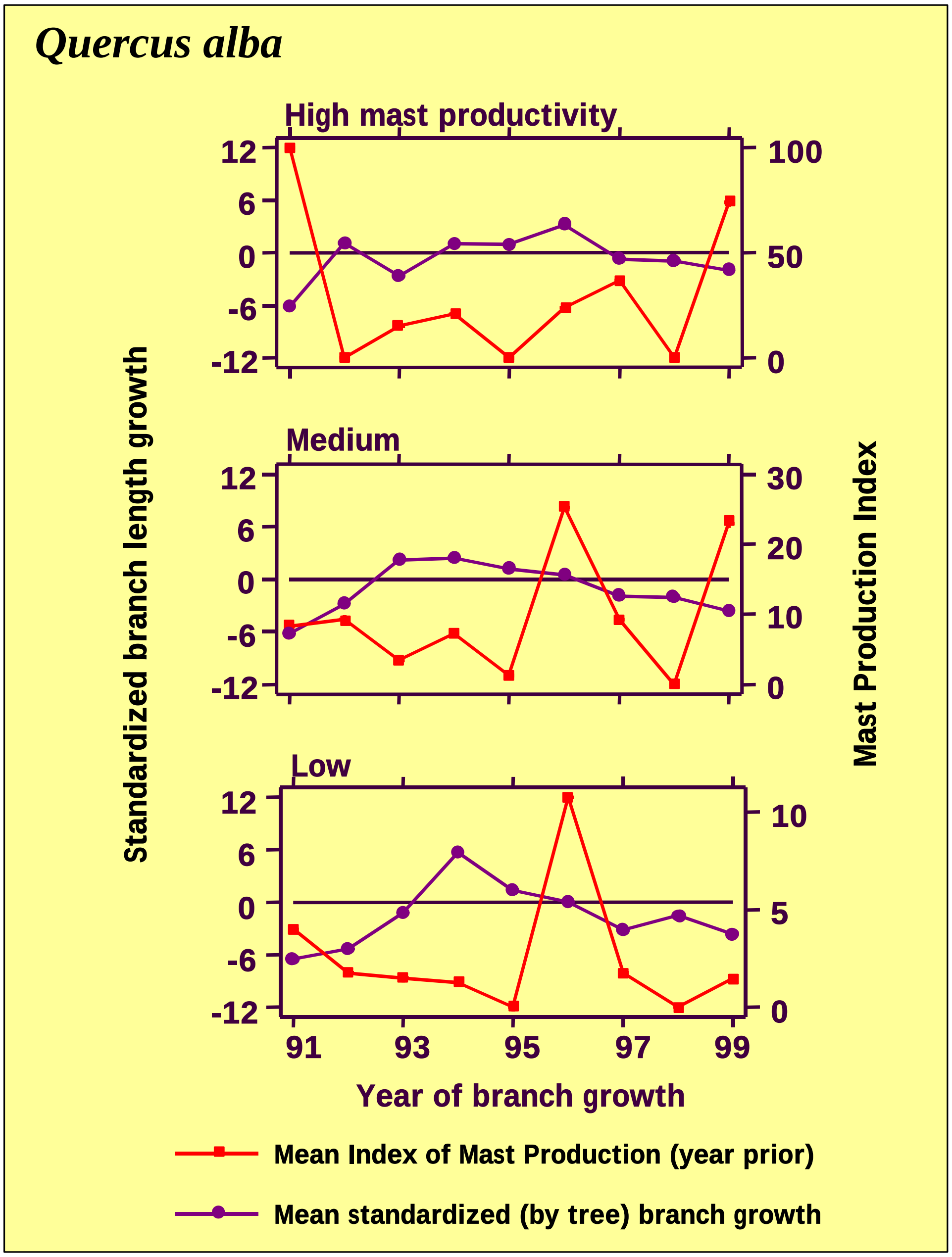

Figure V.3 The mean standardized branch length growth and mast production index by year and productivity group for *Quercus alba*. Branch length was standardized by subtracting the average length growth per tree from each measuremwent

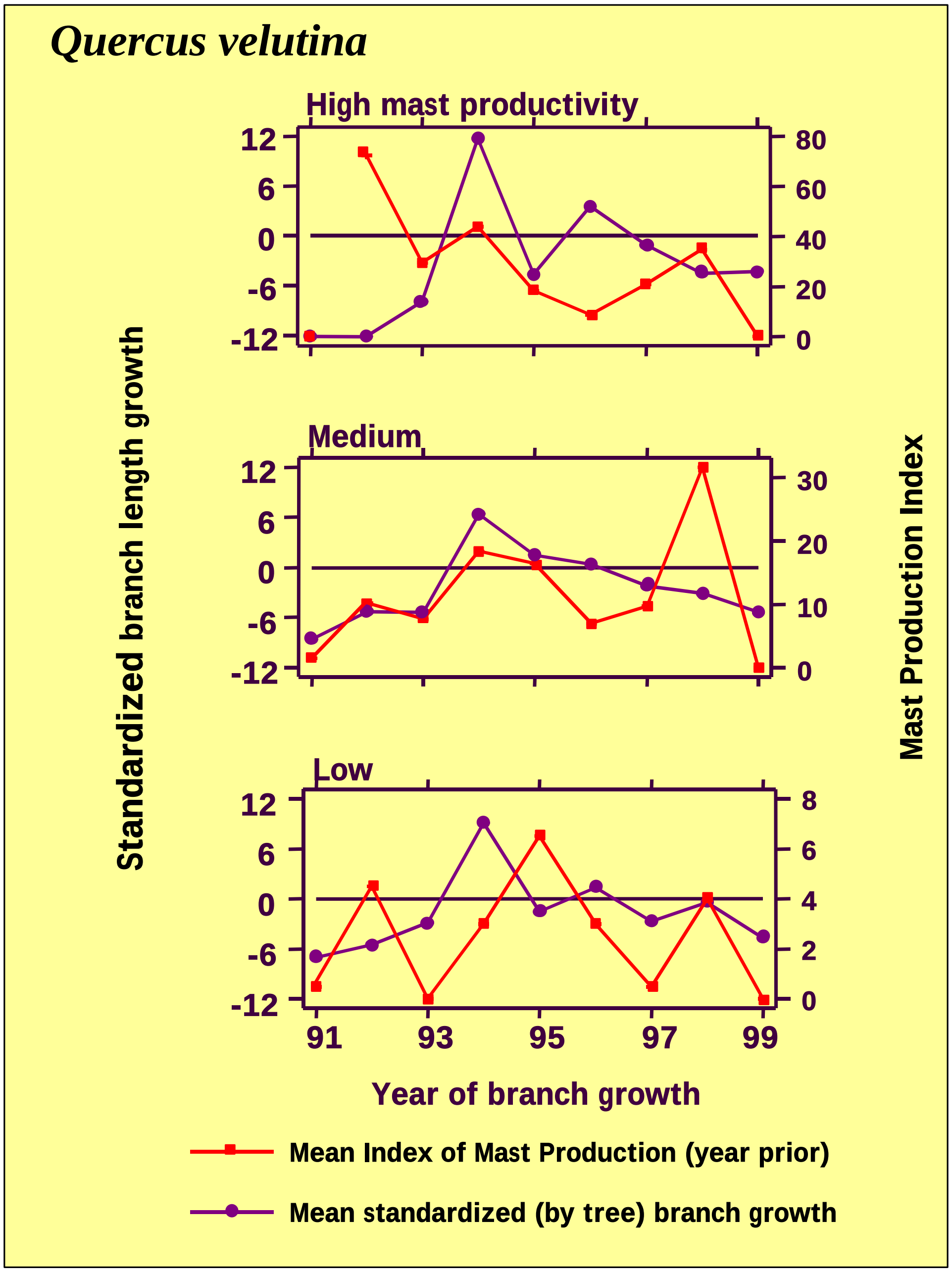

Figure V.4 The mean standardized branch length growth and mast production index by year and productivity group for *Quercus velutina*. Branch length was standardized by subtracting the average length growth per tree from each measuremwent spring freeze resulted in a mast index of 0 for *Q. alba*, but plotted against the year it might be expected to influence shoot growth, 1998. In general, shoot length growth peaked about 1993 with lower but similar growth at the beginning of observations and at the end, 1991 and 1999 respectively. The mast index values do not follow a consistent pattern over the study period.

For the *Q. alba* trees, there appears to be a general increase in shoot growth when there is a decline in mast index. Specific, identifiable weather events influence the patterns. For example, the 1997 freeze might have affected both the mast index and shoot growth. A reduction in shoot growth may either reduce leaf production or place leaves in closer proximity to one another thereby increasing competition for light. Both outcomes would reduce photosynthetic activity and storage of carbohydrates for future growth.

For *Q. velutina*, although more variable, the patterns are similar. There are specific years where there appears to be lower mast indices and correspondingly higher shoot growth the following years, particularly for the trees categorized as low mast producers. However, given all the factors that could contribute to lower shoot growth, and the fact that the actual historical mast production on the branches measured is not known, opportunity for reaching concrete conclusions is limited.

V.3.1 Results: Ex situ measurements of branch growth: Diameter increment

The possible influence of mast production on diameter increment was examined by matching the mast index to the cross-sectional area increment (Figures V.5 and V.6). In general, area increment should be seen to increase exponentially. It is the deviations

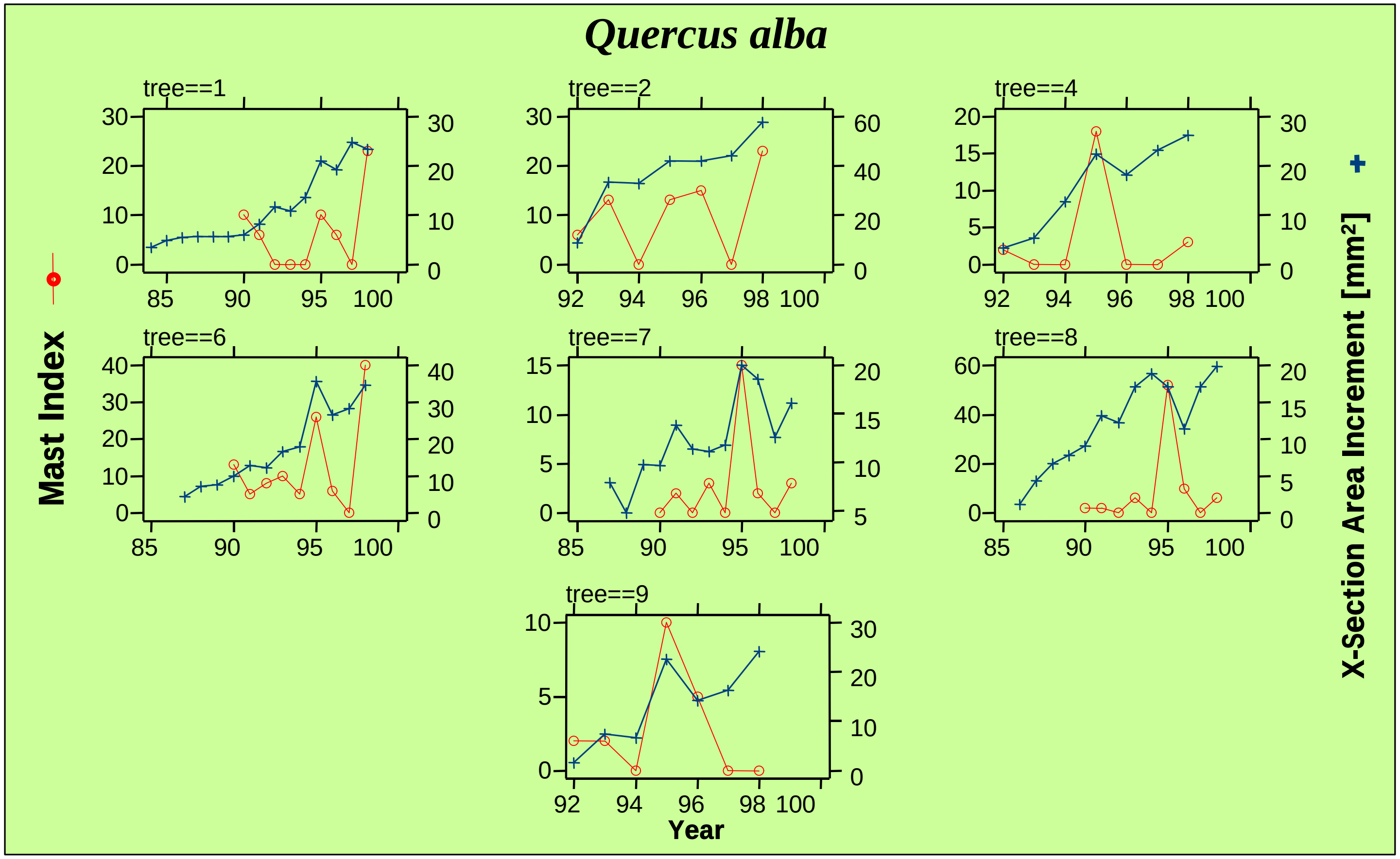

Figure V.5 Radial increment calculated from ring-width measurements by year and tree for branch segments collected in 1999 from seven *Quercus alba* trees.

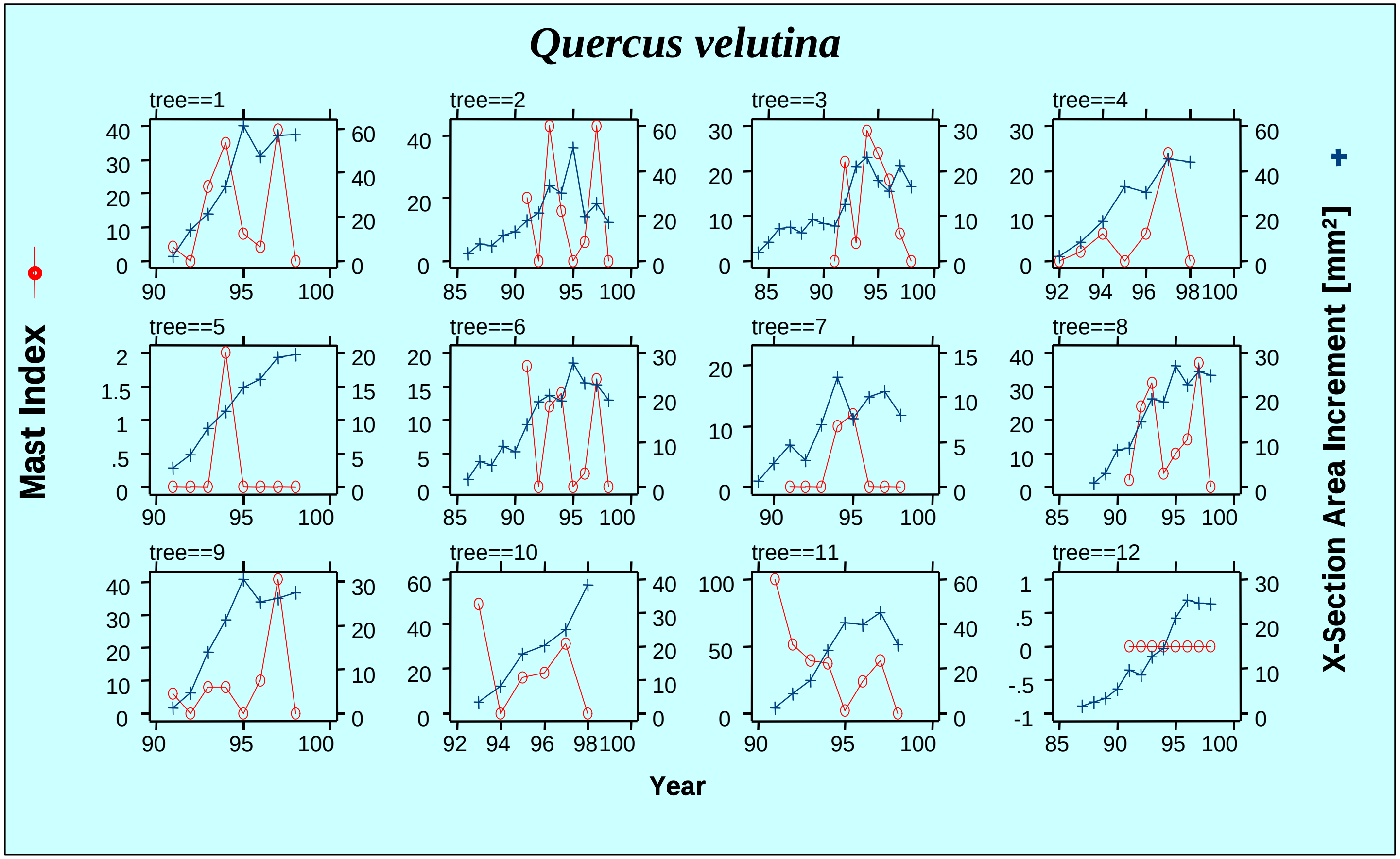

Figure V. 6 Radial increment calculated from ring-width measurements by year and tree for branch segments collected in 1999 from twelve *Quercus velutina* trees.

from the expected exponential growth that are of interest. For example, for *Q. velutina*, tree 12, has a mast index of 0 for all years shows the general increase in diameter with some disturbance in the growth rate occurring between 1995 and 1998. Since, most diameter increment occurs early in the growing season, as with shoot length, the energy amount of energy stored the prior year may influence diameter growth, although the current year acorn growth may also be an influence. Frequently, for *Q. alba* a year of relatively high mast production is followed by a year of reduced diameter increment. Again, this analysis is confounded by potential competing influences.

V.4 CONCLUSIONS

Intensive measurement of changes in diameter on *in situ* branches and correlated acorn production provided the most reliable indicator of the hypothesized tradeoff between reproductive and vegetative growth. More data and intensive data relating shoot growth would be required to quantify the trade-off between acorn production and the subsequent year shoot growth. Perhaps the most appropriate analysis in this sort of situation would be to record a much longer series of observations and utilize time-series analysis techniques that factor the immediate and previous (lagged) influences of climate as well as masting and the general vigor of the study trees. Alternatively, in an experimental design, paired branch ends could be compared after removal of flowers from one branch observing radial growth, acorn development, and shoot growth the following spring.