

SECTION I: INTRODUCTION AND LITERATURE REVIEW

“Interactions between masting trees and their invertebrate and vertebrate seed predators are strong enough to exert the kind of pressures necessary to accentuate environmentally included fluctuation on crop size through evolutionary time into more pronounced adaptive fluctuations of the kind these trees exhibit.”

- Silvertown (1980)

I.1 INTRODUCTION

Masting is the reproductive habit inherent to some tree species where populations produce large seed crops in some years and small seed crops otherwise. This dissertation addresses two areas of mast production: i) formulating an approach to modeling mast production at a landscape scale and ii) understanding how trees allocate resources to mast production by comparing radial and branch length growth from trees monitored for acorn production over nine years. The objective of this section is to introduce the ecology of masting and summarize relevant previous research and other relevant published works. Three sections are allotted to the landscape model. Section II presents a synthesis of previous research along with some new analyses and interpretation to generate parameters and probabilities of mast production indices. Section III is the implementation of the spatial relationships synthesized in Section II with a test-case landscape and the LANDIS output. Section IV introduces annual variability into the masting algorithm. Section V presents the results of an observational study to link branch radial and diameter growth to a mast production index for the previous year.

I 1.1 – THE NATURE OF MASTING

Waller (1979), in an examination of the life-history characteristics of a wide variety of plant forms, hypothesizes that mast fruiting behavior should be restricted to species with high adult survivorship and a low population growth rate. He found that many forest species, including several oaks, adhere to this pattern. Although inconclusive, Silvertown (1980) presented evidence that larger seed crops result in higher

regeneration success, that is, there was a positive correlation between crop size and seed survival for 24 of 59 species and a negative correlation for only 2 of the 59 species.

Many hypotheses regarding the evolutionary advantage of masting behavior have been advanced and tested. Among these are: resource matching, seed dispersal, wind pollination, and predator satiation (LaLonde and Roitberg 1992, Waller 1979, Silvertown, 1980, Koenig *et al.* 1994). For masting behavior to be a successful strategy, trees must be synchronized for both low and high reproduction years (Lalonde and Roitberg 1992). During the interval between large mast crops, predator populations typically decline, thereby increasing the potential for seed to persist in a sound condition and germinate when large mast crops occur.

1.1.1.1. Resource matching

The resource-matching hypothesis states that sufficient resources need to be stored before masting can occur (Silvertown 1980). Among the published research on masting periodicity, high mast production years are usually followed by a year of low mast production. This suggests that the investment in resources to reproduction one year reduces the availability of resources the following year (Silvertown 1980; Sork *et al.* 1993). Similarly, I found no studies that report two consecutive years with high oak mast production. Based on the general frequency of high mast years (1 in 3 to 5 years), if the periodicity is random, consecutive large mast crops should occur about every 20 years.

1.1.1.2. Predator satiation -

The predator satiation hypothesis suggests that plants have evolved the strategy of periodically producing more seed than predator populations can consume, thus increasing the likelihood of seed survival to germination and maturity. Minckler and Janes (1965), in a nine year pin oak study noted that nearly all acorns were infected by weevils during years of poor acorn production and a low percentage were infected during years of high acorn production. Interest in the predator satiation hypothesis is fueled when considered from two perspectives. First, forest managers are interested in masting behavior from the perspective of forest regeneration. If seed predators are not sated, most seed will be consumed and not available for regeneration. Second, wildlife managers are interested in masting since the animal populations they manage will be affected by the quantity of mast available for food.

1.1.1.2.1. Predator satiation: Masting and wildlife -

Many studies have shown a relationship between animal population size and masting behavior. Wildlife managers in Missouri are interested in predicting mast production since the populations of important game species, squirrel, deer and turkey, are influenced by masting behavior. Nixon (1969) found a decrease in the squirrel population following a severe mast crop failure due to a late spring frost in Ohio. Hannon (1987) noted a similar relationship between acorn production levels and local woodpecker populations as well as increased aggressive behavior between woodpecker groups. Harlow (1975) found that in West Virginia, 76 percent of the diet of deer

consisted of acorns when acorns were abundant. Wolfe (1996), recording a 14 year time-series including 3 distinctively larger mast crops, noted a positive correlation between the crop and the size of the rodent population of the subsequent year. In addition, acorns were not available during years of low acorn production in January whereas acorns were available for food (and presumably for oak regeneration) throughout the winter during years of high acorn production. A study in Virginia documented that deer consumed most (70 percent) of the mast in the Autumn soon after falling while later in the winter, acorns are a major source of food for squirrel species (*Sciurus* spp.) (McShea and Schwede 1993). Increased mast may lead to increased deer population density and increased mast consumption in the autumn and decreased population densities of other species that rely on mast availability for late winter survival.

1.1.1.2.2. Predator satiation: Complex community relationships -

Ostfeld *et al.* (1996) described a complex relationship among mast availability, mice and chipmunks, deer, ticks, gypsy moths, and Lyme disease. Interestingly, the authors suggest that a low mast crop leads to a lower rodent population the following year and the subsequent affect on the moth population leads to lower acorn production. That is, one moth predator population (squirrels) is lower, thus, the gypsy moth population is higher and a higher amount of foliage is consumed leading to lower carbon fixation and, subsequently, lower mast production. One of the results of masting as a reproductive strategy is to limit wildlife populations by decreasing the fitness of wildlife species during low mast years (Ostfeld *et al.* 1996). Thus, when masting years do occur, fewer herbivores are present to graze on seeds. In New Zealand, a complex predator-prey

relationship exists that ultimately may affect endangered species. When beech trees produce a large crop of seeds, the mouse population increases. The mouse population is the major prey of stoats (an ermine), thus the stoat population flourishes. When the mouse population declines as a consequence of predation, the stoats prey upon birds and bats (Wilson *et al.* 1998).

1.1.1.3. Wind Pollination -

The wind pollination hypothesis states that species that rely on pollen dispersal and deposition by the wind have developed synchronized reproductive behavior to increase the likelihood of pollination success and cross-pollination. Oaks are wind pollinated; however, this may be a mechanism by which masting is implemented as well as a means of increasing pollination success. That is, climate conditions must be favorable during the short period of pollen dispersal for pollination to succeed (Cecich and Sullivan 1999; Wolgast and Stout 1977).

1.1.1.4. Seed Dispersal -

The seed dispersal hypothesis suggests masting behavior attracts animal dispersers, thus increasing the dispersal of seed and increasing the range of a plant population. The seed dispersal hypothesis would perhaps be an appropriate strategy for plants that produce seed that are capable of surviving to be viable after passage through the gut of an animal. Acorns would not be viable and in a comparison of these four hypotheses, Koenig *et al.* (1994) found little support for the seed dispersal hypothesis among California oaks. Koenig also did not find support for the resource-matching

hypothesis. Each masting species follows a different evolutionary path; thus, all the theories can be true but each more true for some species than for others.

1.1.1.5. Variability in masting among years -

Regardless of the evolutionary strategies leading to masting behavior, masting undoubtedly exists. Johnson (1975) in two consecutive years observed an estimated 300 and 153,000 acorns per hectare in a white oak stand in Illinois. VanGilder (1997) reporting on the results from 130 plots in a mast study in Missouri found averages ranging from about 23,000 to 165,000 acorns per hectare for 1993 through 1994. In a study of turkey food sources in Arkansas there was no acorn production in five of nineteen years. The interval between masting years can range from 2 to 10 years. Ultimately, the cause of evolving masting behavior is related to increasing the success of regeneration, but the mechanism for implementing this behavior can include responses to weather and gradual accumulation of carbohydrates (Silvertown 1980). Sork *et al.* (1993) found that the size of the acorn crop for several oak species in Missouri had a major negative influence on the subsequent year's crop and that weather conditions had only a minor influence on mast production.

I would suggest that both weather and resource storage are integral components of masting behavior. That is, weather is one of the mechanisms by which masting is implemented. Weather components that might be selected as mechanisms for moderating mast production include the tendency of oaks to flower in early spring while still vulnerable to freezing damage. However, since oaks are a species of tropical origin, the early flowering habit could be a trait remaining from the migration toward the north.

In fact, a study in Pennsylvania found that in 50 years, only 8 percent of the complete acorn crop failures and 8 percent of the partial failures could be attributed to freezing (Sharpe and Sprague 1967). Alternatively, Auchmoody *et al.* (1993) in another study in Pennsylvania found that acorn crop failure could be attributed to freezing temperatures during the flowering stage in 3 of 5 years. Uhlig and Wilson (1952) evaluated a mast index for West Virginia and found a correlation between May minimum temperatures and the index. The influence of freezing conditions may be particularly important in Missouri. Potter and Cate (1999) estimate that the Ozark Mountains of Missouri experience more late spring freezes than any other area in the northeast quarter of the U.S. Hail and severe weather can affect acorn production (Cecich and Sullivan 1999). Relative humidity during the pollination period is another component of weather that has been shown to be a factor influencing acorn production (Sharp and Chisman 1961; Wolgast and Stout 1977). Whether due to evolutionary selection or serendipity, spring freezing, relative humidity, hail, and rain have been shown to be influential and therefore should be considered in predicting potential and realized acorn production.

1.1.1.6. Variability in masting within years -

In addition to among-year variation in acorn production, there is also variation among species and among individual trees of a species. Factors affecting acorn production among individual trees include: location, size, and inherent genetic variability. In some circumstances location could account for different responses to weather. VanGilder (1997) has noted higher acorn production on Ozark ridge tops perhaps due to lower incidence of late spring freeze or higher probability of lower humidity favoring

pollen dispersal. Dominant and co-dominant trees have been shown to produce more acorns; thus canopy position is a factor. Branch location within a tree has also been shown to affect acorn production. Post (1998) in a study of flowering and crown competition in a *Q. rubra* seed orchard noted higher acorn production on the south side of trees, perhaps due to higher photosynthetic activity and carbon storage on these branches.. At the branch level, decreased vigor of older branches leads to reduced vascular tissue and increased isolation from the entire tree, resulting in lower photosynthate availability for fruit production (Sprugel *et al.* 1991). Generally speaking, oak trees begin producing acorns at about 20 to 25 years in age under favorable conditions (Waller 1979). Although age is not a reliable indicator of tree size (Loewenstein *et al.* 2000), the measure of tree size usually reported is diameter. Aside from observing individual tree acorn production (Healy *et al.* 1999), diameter is the best predictor of acorn production. Acorn production increases with diameter, reaches a maximum level, and then declines. The decline is perhaps due to competition for resources, particularly carbohydrates needed for radial growth, a biological necessity that increases exponentially as tree surface area increases. Downs (1944) characterized the diameter and acorn production relationship for several oak species using 7 years of data (Figure I.1) and other studies also have shown this pattern (Goodrum 1971; Greenberg 2000; Auchmoody 1993)

Most studies involving observation of individual trees note the wide range of variability in acorn production among trees of a species. Although spanning only two years, Post (1998) found that 4 out of her 22 original study trees did not flower. One of the 23 white and black oaks studied by Cecich (1998) over nine years was consistently

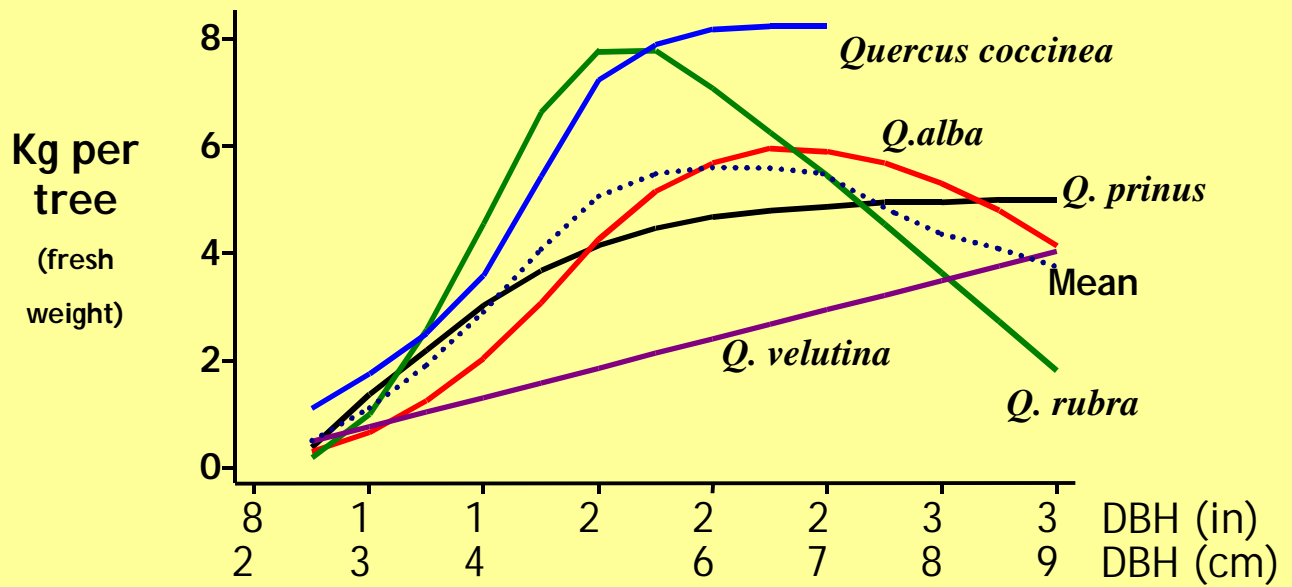


Figure I.1 Acorn production as a function of diameter for a 7 year study in North Carolina (Downs 1944)

one of the highest producers of flowers and immature acorns, yet all acorns aborted before maturing. Among 12 white oaks studied in Missouri in 1981, Shelburne (1983) estimated the acorn production ranged from 12 acorns to over 3500 acorns per tree. Some studies addressing acorn production have suggested the best method of ensuring high mast yield is to observe the behavior of trees for several years and select for production (Healy *et al.* 1999; Farmer 1981).

I 1.2 THE SCOPE AND SCALE OF THIS RESEARCH

The remainder of this section (Section I) is devoted to summarizing relevant studies and information as they relate to mast production and the remainder of this document. Although there are many genera that produce mast and display periodic synchronous production, because of their relative importance in Missouri, I will focus on the oak species. This thesis addresses three areas of the study of mast production:

- Section II. Characterization of the probabilities and quantity of acorn crop production.
- Section III. Modeling acorn production across a landscape.
- Section IV. Masting behavior as a potential resource sink.

The first of the remaining sections (Section II) is a synthesis of data related to mast production presented in this literature review along with newly analyzed data. The ultimate objective of this synthesis is to generate factors at a scale appropriate for use in predicting acorn production using the output data and data format generated by the LANDIS landscape model of forest change. More detail than is required by LANDIS is presented for the purpose of justifying the parameters and for potential use in more

specific models. Section III presents the implementation of these parameters for LANDIS output. The landscape perspective addresses the interests of managers and researchers charged with considering the long-term consequences of management practices and changing landscapes over large areas.

The third topic, somewhat removed in scope and scale, addresses masting as an investment of resources from an ecophysiological viewpoint. Branches from trees monitored for flower and acorn production for 9 years were collected and subjected to a modified stem analysis to examine the relationships between vegetative growth and acorn production.

I.2 Sequence of Acorn development

I.2.1. Flower initiation-

Flower initiation, that is, assignment of a bud to a flowering fate rather than a vegetative growth fate, for oaks occurs in late summer of the year prior to the appearance of the flower in the spring. The signals responsible for bud fate assignment are not yet defined for oaks. In a study of oak flowering, the mast production index was not related to the number of flowers initiated in eight *Q. alba* trees in subsequent years (Cecich, unpublished data). Two classes of meristematic identity genes have been identified for the model species *Arabidopsis* spp.:

Shoot meristem ID genes: genes that when expressed seem to transform the meristematic tissue into one which produces shoot or leaf-like vegetative structures. These include TERMINAL FLOWER 1 (TFL1) that represses the following gene class:

Flower meristem ID genes: genes that have been shown to lead meristem tissue toward becoming flowers, including APETALA1 (AP1) and the interestingly named gene LEAFY. These genes are somewhat redundant in this stage but AP1 is involved with later development.

The cues that trigger the flower initiation process for *Arabidopsis* are genetically regulated and associated with environmental conditions, such as photoperiod, light quality, and temperature as well as plant age (Mizukami and Ma 1997; Yanofsky 1995; Liljegren *et al.* 1999).

1.2.2. Flower emergence -

For all oaks in the temperate region, flowers emerge in early spring between March and May specifically as a function of cumulative heat sum. Staminate flowers (catkins) appear first, followed 5 to 10 days later by pistillate flowers (Rogers, 1990). The staminate inflorescence is initiated from the axil of a bud scale on the current year's shoot growth. The pistillate flowers are found at the leaf axil, usually in pairs. Wind dispersal (anemophily) is the method of pollen dispersal and deposition.

1.2.3. Pollen dispersal -

Pollen is disseminated over a period of about 3 days and may be delayed under wet weather conditions. Pollen fate is the subject of a model presented by Inouye *et al.* (1994). In this model, the authors identified many of the sources of pollination failure including pollen loss by herbivory before and after dispersal, ill-timed pollen deposition, incompatible pollen, and aborted seeds and fruit. Of these factors, the timing of pollen dispersal relative to the availability of receptive pistillate flowers is the only factor in

pollination considered to be suitable for modeling from a top-down approach. Pistillate flowers of the white oak group (subgenus *Lepidobalanus*) are fertilized shortly after pollination and acorns develop and mature in the late summer following fertilization, fall from the tree after about 25 days, and germinate soon after. Staminate flowers from trees of the red oak group (subgenus *Erythrobalanus*), once pollinated, begin to develop a pollen tube but pollen tube completion and fertilization is delayed for 1 year, after which maturation of acorns occurs. If not fertilized, the flowers abscise.

1.2.4. Modeling flowering dynamics –

Prediction of the acorn crop is the ultimate objective of the models in this study. Figure 1.2 expresses the acorn crop as the sum of the red- and white- oak group acorn production as affected by the conditions under which the flowers and acorns of each group developed. For example, a late spring freeze during the current year may affect acorn production of the white oak group for the current year by damaging the relatively vulnerable catkins, but have little or no influence on the dormant red oak pistillate flowers that were pollinated the previous year.

Anthers open as relative humidity decreases and close with increasing relative humidity (Wolgast and Stout 1977). Therefore, long periods of high relative humidity or rain may result in pollination failure. Dry winds and late-spring freezes can affect pollination and flower survival. Some studies have shown that acorn crops are larger when there is a warm period during pollen shed and flowering followed by a 10 to 20 day cooler period (Sharp and Sprague, 1967; Sharp and Chisman, 1961; Sork *et al.*, 1993). Black oak (*Q. velutina*) has been found to flower in mid-Missouri about one week earlier

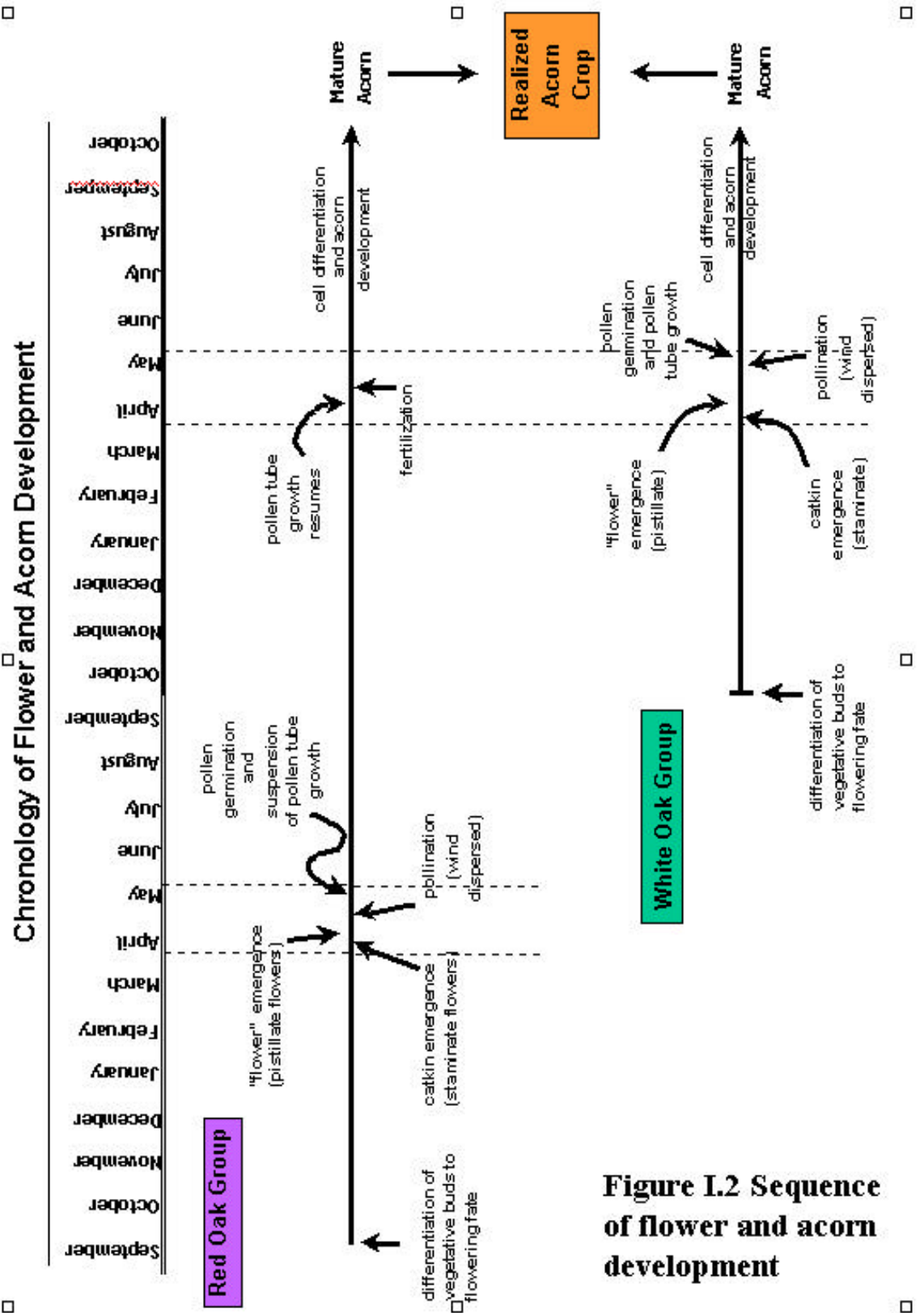


Figure I.2 Sequence of flower and acorn development

than white oak (*Q. alba*) (Cecich, per. comm.). Thus, variations in weather may result in differences in pollination success, that is, the degree of success or failure of a white acorn crop last year is not necessarily an indication of red oak acorn production this year.

I.3 MISSOURI FACTORS FOR THIS STUDY

I.3.1 Sources of Information

The basic silvics of the important oak species were derived primarily from *Silvics of North America: Volume 2* in which authors with a particular expertise on a species were responsible for compiling available information on that species. Therefore, both the perspective of the authors and the availability of data on a species affect the quantity and quality of the descriptions. The descriptions have been compiled with the foreknowledge that the information is intended for use in a model of mast production. Particular attention is given to those factors thought to affect masting. Silvics of the species are used to identify characteristics that are similar among species, thus allowing species be placed in classes with common ecological requirements or common responses to environmental factors. Likewise, species that are uniquely suited to a particular environment or display a unique response to environmental conditions can be identified and factored appropriately. Along with the relevant silvics of each species, the abundance and distribution of the species throughout Missouri is described. The abundance, geographical, and physiographical distributions are described to help identify species that are important components of Missouri forests and species that may be important due to the environments where they are shown to occur. For example,.

Table I.1: An estimate of the abundance of oaks greater than 1 inch in diameter in Missouri (U.S.F.S. FIA, 1989).

Species	Common Name	Acronym	FIA Code	Oak Group* (subgenus)	Millions of Trees	Percent of All Oaks
<i>Quercus alba</i>	White oak	<i>Qa</i>	80	White	77	27.94
<i>Q. velutina</i>	Black oak	<i>Qv</i>	83	Red	70	25.15
<i>Q. stellata</i>	Post oak	<i>Qst</i>	83	White	66	23.68
<i>Q. marilandica</i>	Blackjack oak	<i>Qmr</i>	82	Red	22	7.99
<i>Q. coccinea</i>	Scarlet oak	<i>Qc</i>	80	Red	15	5.56
<i>Q. rubra</i>	Northern red oak	<i>Qr</i>	83	Red	8	3.18
<i>Q. muehlenbergii</i>	Chinkapin oak	<i>Qmu</i>	82	White	6	2.40
<i>Q. imbricaria</i>	Shingle oak	<i>Qi</i>	81	Red	5	1.90
<i>Q. palustris</i>	Pin oak	<i>Qpa</i>	83	Red	2	0.74
<i>Q. falcata v. falcata</i>	Southern red oak	<i>Off</i>	81	Red	1	0.50
<i>Q. macrocarpa</i>	Bur oak	<i>Qma</i>	82	White	1	0.44
<i>Q. bicolor</i>	Swamp white oak	<i>Qb</i>	80	White	1	0.36
<i>Q. lyrata</i>	Overcup oak	<i>Ql</i>	82	White	2	0.06
<i>Q. michauxii</i>	Swamp chestnut oak	<i>Qmi</i>	82	White	0.9	0.03
<i>Q. shumardii</i>	Shumard oak	<i>Qsh</i>	83	Red	0.5	0.02
<i>Q. falcata v.</i>	Cherrybark oak	<i>Qfg</i>	81	Red	0.5	0.02
<i>Q. phellos</i>	Willow oak	<i>Qph</i>	83	Red	0.2	0.01
<i>Q. ellipsoidalis</i>	Northern pin oak	<i>Qe</i>	80	Red	0.	0.01
<i>Q. prinus</i>	Chestnut oak	<i>Qpr</i>	83	White	0.1	0.01
All Oak						
* White <i>Lipidobalan</i> , Red <i>Erythrobalan</i>						

Q. palustris (pin oak), comprising only 0.74% of Missouri oaks, is a relatively unimportant component of Missouri forests in terms of abundance (Table I.1); but the capacity of this species to withstand periodic flooding increases the overall importance of the species. These descriptions of species have been kept separated to facilitate extending the LANDIS module algorithm to other regions where oak species are present. Application and classification are addressed in Section II and Section III of this document.

The primary source of quantitative data for the species descriptions is the Internet Web Based U.S. Forest Service Forest Inventory and Analysis Data Base Retrieval System (Hansen *et al.* 1992). The inventory protocol and database has been standardized for the eastern states (East Wide Database). Basing the model algorithms and parameters on this source of data will facilitate application of the methods beyond the borders of Missouri. In the most recently completed inventory of Missouri (1989), there were 17,270 plots of which 5,077 were classified as forestland. About 178,000 trees (Diameter > 1 inch at 1.3 m in height), were measured. Plot descriptors relevant to this study include, location (latitude and longitude), forest type, aspect, “Physiographic” class (a description of soil moisture characteristics), and slope. Notable tree traits include species and diameter. In addition to FIA data, pre-treatment data for the Missouri Ozark Forest Ecosystem Project (MOFEP) were utilized (Shifley and Brookshire 2000; Brookshire and Shifley 1997). Measurements were made on about 96,000 trees distributed among 645 plots. The disparity between the FIA and MOFEP ratio of sample trees to plot is related to the sampling design, *i.e.* point- versus fixed area-sampling. For each set of data, the values for the observations are expanded differently and values provided by the table

generator were used unless specified otherwise for FIA and simply weighted by sample area for MOFEP data.

I.3.2 Oak Species in Missouri

Oak species are of tropical origin. There are about 500 species worldwide and the number of oak species decreases with distance from the equator increases (Dickson 1996). There are about 200 oak species in the Western Hemisphere; there are 125 species found in Mexico, about 60 species found throughout the U.S. and only 7 species as far north as southern Minnesota and Wisconsin. The 1989 FIA inventory reported 19 species of oaks in Missouri

As a group, in terms of the number of trees, oaks comprise about 38 percent of the trees greater than 1 inch (2.5 cm) in DBH on timberland in Missouri (Table I. 2) of the remaining 62 percent, 8 percent are softwood species. The oaks are somewhat equally divided between trees of the white oak group and the red oaks. The oak species occupy the majority of the larger size classes. Oaks comprise only about 28 percent of all trees in the 5 cm diameter class, but greater than 70 percent of trees in the 30 to 70 cm range (Figure I.3). Three of the 19 oak species found in Missouri comprise about 77 percent of the oak trees (*Q. alba*, *Q. velutina*, and *Q. stellata*). Brief descriptions of the silvics of these three species and four others (*Q. marilandica*, *Q. coccinea*, *Q. rubra*, and *Q. palustris*) are included below. The remaining species comprise less than 6 percent of the oaks and less than 2 percent of all the trees in Missouri.

Table I.2: Frequency of trees in common species groups in Missouri [all trees >2.54 cm in diameter at 1.3 m in height] (FIA 1989).

Species	Millions of Trees	Percentage of Total
Other red oak	1,167	15.9%
Select white oak	869	11.8%
Other white oak	662	9.0%
Select red oak	90	1.2%
All Oaks	2789	37.9%
Other soft hardwood	1,133	15.4%
Hickory	1,103	15.0%
Other hard hardwood	760	10.3%
Other softwood	384	5.2%
Noncommercial	299	4.1%
Ashes	213	2.9%
Shortleaf-loblolly pine	163	2.2%
Hard maple	151	2.0%
Soft maple	132	1.8%
Tupelo-blackgum	129	1.8%
Black walnut	84	1.1%
Basswood	10	0.1%
Cottonwoods-aspen	6	0.1%
Sweetgum	4	0.1%
Eastern white-red pine	2	0.0%
Yellow-poplar	1	0.0%
Beech	1	0.0%
Other pine	1	0.0%
Cypress	0	0.0%
All		

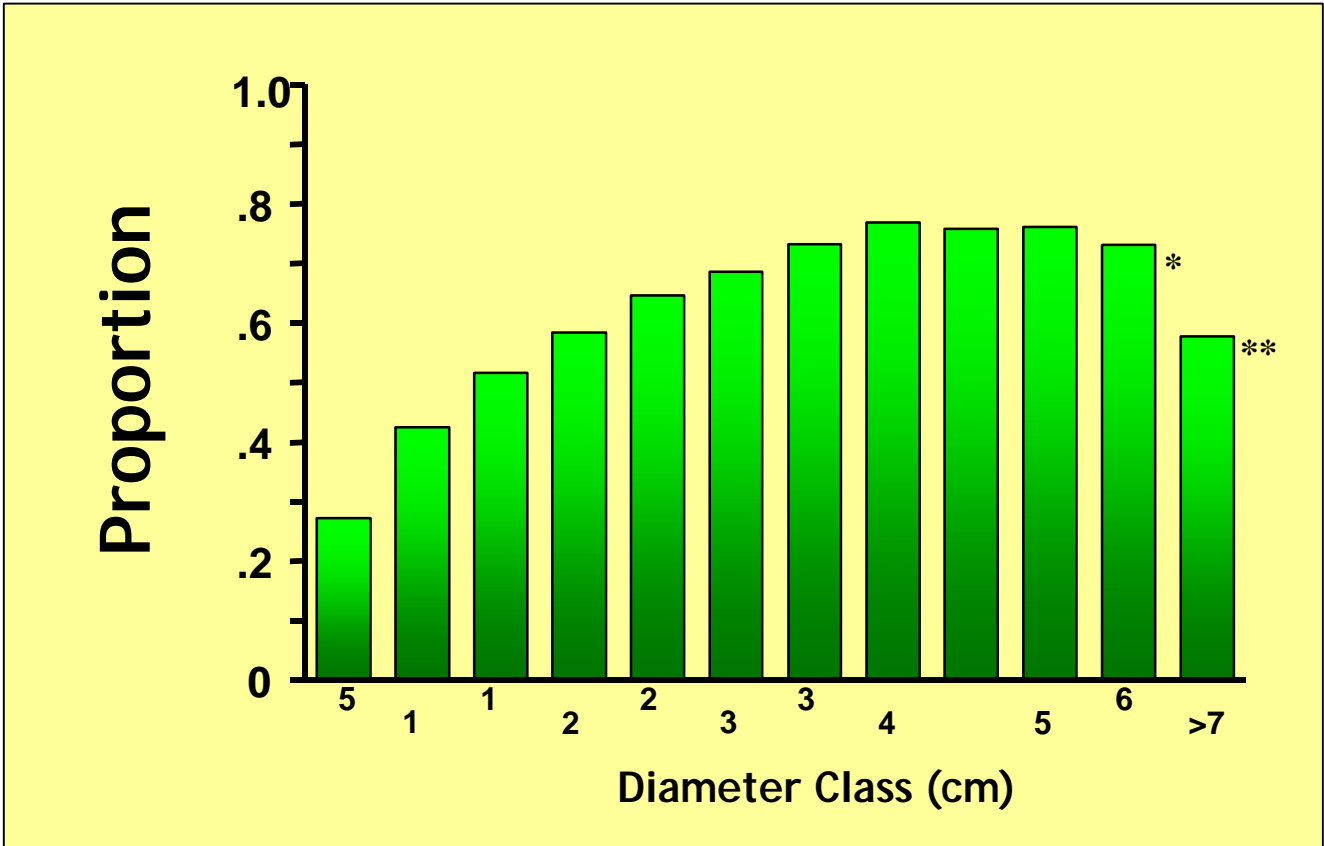


Figure I.3. Proportion oak component of each diameter class in Missouri (FIA 1989). Labels indicate mid-point of the class spanning about 10 cm except * which is 20 cm and ** which is all trees greater than about 74 cm.

I.3.2.1. *Quercus alba* –

In the U.S., *Q. alba* (white oak) is found throughout the eastern states as far north as southern Maine and southern Minnesota and as far south as northern Florida (Rogers 1990). It is generally absent at the higher elevations of the Appalachian mountain range. This species is found under a wide range of climatic conditions. Within this region, annual precipitation ranges from 760 mm in southern Minnesota to 2000 mm in the southern Appalachians. Major site factors that influence growth include latitude, aspect, and topography. Across its entire range, *Q. alba* grows best on north and east slopes and coves but grows well on moderately dry slopes and ridges with shallow soils. It is more abundant on west and south slopes but smaller in stature.

In Missouri, *Q. alba* is the most abundant of the oak species. With an estimated 779 million trees, it comprises about 28 percent of all oaks (Table I.1) and is found throughout the state. The highest frequency of white oaks is in the south central region of the state (Figure I.4). On the MOFEP sites in the Ozark Mountains, about 47% of the inventoried trees were *Q. alba* (Table I.3). About 89 percent of the white oak trees sampled in the 1989 FIA survey were found on either xeromesic or mesic sites (Table I.4). Although, about 86 percent of the inventory plots were in these two classes of soil moisture condition (Table I.5), a large number of the inventoried trees were not assigned to a soil-moisture classes (9.6 percent) and fewer trees by a factor of 10 were assigned to the hydric and hydromesic classes (0.1 and 0.2 percent) than would be expected given the number of plots in these classes.

The FIA plot aspect data given in azimuth degrees was separated into eight classes (Figure I.5). The plots are evenly distributed among the eight aspect classes.

Table I.3: Distribution of species on MoFEP sites (all trees μ 5 inches DBH).

Species	Inventory Frequency ¹	Percent	Trees Per Acre ²	Trees Per Hectare
<i>Quercus velutina</i>	10994	22.7	34.1	84.2
<i>Q. alba</i>	10376	21.4	32.2	79.5
<i>Q. coccinea</i>	9910	20.4	30.7	75.9
<i>Q. stellata</i>	2979	6.1	9.2	22.8
<i>Q. marilandica</i>	615	1.3	1.9	4.7
<i>Q. muehlbergii</i>	395	0.8	1.2	3.0
<i>Quercus</i> spp.	31	0.1	0.10	0.24
<i>Q. rubra</i>	5	0.0	0.016	0.04
<i>Q. shumardii</i>	5	0.0	0.016	0.04
<i>Pinus echinata</i>	4552	9.4	14.1	34.9
<i>Carya texana</i>	2259	4.7	7.0	17.3
<i>C. glabra</i>	2104	4.3	6.5	16.1
<i>C. tomentosa</i>	2067	4.3	6.4	15.8
<i>Nyssa sylvatica</i>	647	1.3	2.0	5.0
<i>Juglans nigra</i>	277	0.6	0.86	2.1
<i>Cornus florida</i>	273	0.6	0.85	2.1
<i>Ulmus rubra</i>	171	0.4	0.53	1.3
<i>Fraxinus americana</i>	141	0.3	0.44	1.1
<i>Acer rubrum</i>	104	0.2	0.32	0.80
<i>Ulmus alata</i>	100	0.2	0.31	0.77
<i>Carya cordiformis</i>	85	0.2	0.26	0.65
<i>Juniperus virginiana</i>	79	0.2	0.24	0.61
<i>Sassafras albidum</i>	79	0.2	0.24	0.61
<i>Acer saccharum</i>	63	0.1	0.20	0.48
<i>Morus rubra</i>	35	0.1	0.11	0.27
<i>Prunus serotina</i>	24	0.1	0.07	0.18
<i>Carya ovata</i>	20	0.0	0.06	0.15
<i>Cercis canadensis</i>	20	0.0	0.06	0.15
<i>Ulmus americana</i>	19	0.0	0.06	0.15
<i>Diospyros virginiana</i>	12	0.0	0.037	0.09
<i>Bumelia lanuginosa</i>	11	0.0	0.034	0.08
<i>Amelanchier arborea</i>	8	0.0	0.025	0.06
<i>Fraxinus pennsylvanica</i>	8	0.0	0.025	0.06

Table I.3 (continued): Distribution of species on MoFEP sites (all trees ≥ 5 inches DBH).

<i>Gleditsia triacanthos</i>	8	0.0	0.025	0.06
<i>Celtis</i> spp.	6	0.0	0.019	0.05
<i>C. occidentalis</i>	5	0.0	0.016	0.04
<i>Rhus glabra</i>	2	0.0	0.006	0.02
<i>Carpinus caroliniana</i>	1	0.0	0.003	0.01
<i>Crataegus</i> spp.	1	0.0	0.003	0.01
<i>Prunus americana</i>	1	0.0	0.003	0.01
<i>Rhamnus caroliniana</i>	1	0.0	0.003	0.01

1. Number of trees measured among 645 0.5 acre plots
2. Inventory $N * 2 / 645$ plots

Table I.4a: Distribution of oaks among FIA physiographic land classes (all trees > 1 inch). The plot distribution row is the percentage of the total number of FIA plots per class (FIA 1989). A key to the acronyms is given in Table I.1.

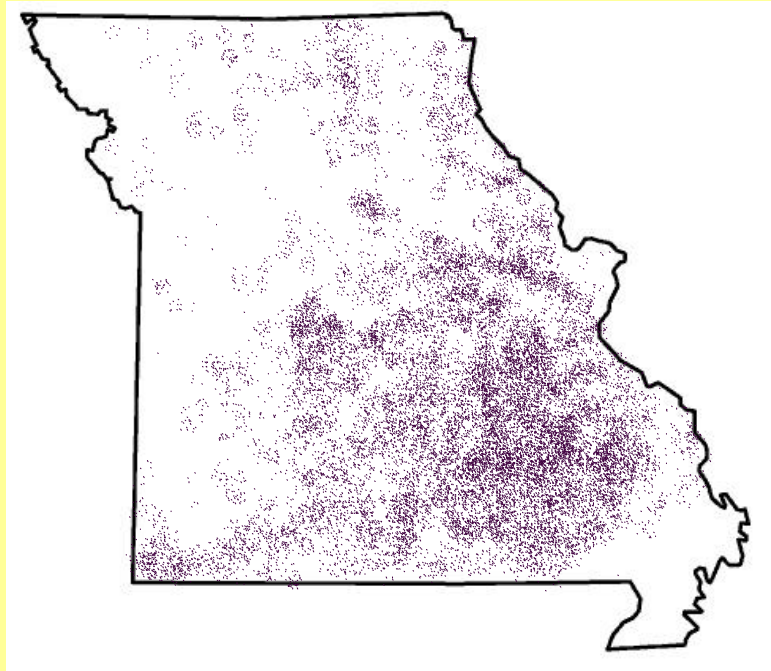
Species Acronym [oaks]	Physiographic Class						Number of Trees Measured
	Unassigned	3 Xeric	4 Xeromesic	5 Mesic	6 Hydromesic	7 Hydric	
<i>Qv</i>	10.7%	1.1%	68.8%	19.1%	0.2%	0.1%	22724
<i>Qa</i>	9.6%	0.5%	61.7%	28.0%	0.2%	0.1%	22587
<i>Qst</i>	9.4%	2.3%	69.8%	18.1%	0.4%	0.0%	17858
<i>Qmr</i>	12.1%	3.6%	74.0%	10.2%	0.2%	0.0%	5327
<i>Qc</i>	8.6%	0.9%	76.8%	13.4%	0.1%	0.1%	5079
<i>Qr</i>	7.0%	1.1%	54.8%	34.9%	2.0%	0.2%	3830
<i>Qmu</i>	5.0%	3.9%	62.2%	27.7%	1.1%	0.1%	1947
<i>Qi</i>	0.5%	0.1%	19.8%	75.1%	3.7%	0.9%	1367
<i>Qpa</i>	3.2%	0.0%	4.4%	63.6%	23.7%	5.1%	803
<i>Qma</i>	0.9%	0.0%	13.3%	78.3%	5.0%	2.4%	540
<i>Qff</i>	8.1%	2.4%	72.9%	16.2%	0.5%	0.0%	420
<i>Qb</i>	1.0%	0.0%	10.0%	68.9%	16.3%	3.9%	411
<i>Ql</i>	9.5%	0.0%	1.2%	17.9%	0.0%	71.4%	84
<i>Qsh</i>	11.5%	1.9%	40.4%	44.2%	1.9%	0.0%	52
<i>Qph</i>	50.0%	0.0%	0.0%	13.6%	29.5%	6.8%	44
<i>Qfp</i>	4.8%	0.0%	19.0%	21.4%	19.0%	35.7%	42
<i>Qmi</i>	12.1%	0.0%	27.3%	57.6%	3.0%	0.0%	33
<i>Qe</i>	0.0%	0.0%	0.0%	66.7%	33.3%	0.0%	3
<i>Qpr</i>	0.0%	0.0%	66.7%	33.3%	0.0%	0.0%	3
<i>Qn</i>	100.0%	0.0%	0.0%	0.0%	0.0%	0.0%	1
Plot Dist.	8.5%	1.2%	55.5%	30.6%	3.0%	1.1%	
Number of Trees Measured	7832	1139	53953	19357	634	240	83155

Table I.4b: Distribution of oaks among FIA physiographic land classes (all trees > 1 inch). These values indicate the difference between the observed distribution of trees among classes and the overall distribution of plots among classes. Negative values (in parentheses) indicate fewer trees than would be expected if evenly distributed, positive values indicate a greater number of trees per class than would be expected See table I.1 for the species acronym key (FIA 1989).

Species Acronym [oaks]	Physiographic Class					
	Unassigned	3 Xeric	4 Xeromesic	5 Mesic	6 Hydromesic	7 Hydric
<i>Qv</i>	2.2	(0.1)	13.3	(11.5)	(2.8)	(1.0)
<i>Qa</i>	1.1	(0.7)	6.2	(2.6)	(2.8)	(1.0)
<i>Qst</i>	0.9	1.1	14.3	(12.5)	(2.6)	(1.1)
<i>Qmr</i>	3.6	2.4	18.5	(20.4)	(2.8)	(1.1)
<i>Qc</i>	0.1	(0.3)	21.3	(17.2)	(2.9)	(1.0)
<i>Qr</i>	(1.5)	(0.1)	(0.7)	4.3	(1.0)	(0.9)
<i>Qmu</i>	(3.5)	2.7	6.7	(2.9)	(1.9)	(1.0)
<i>Qi</i>	(8.0)	(1.1)	(35.7)	44.5	0.7	(0.2)
<i>Qpa</i>	(5.3)	(1.2)	(51.1)	33.0	20.7	4.0
<i>Qma</i>	(7.6)	(1.2)	(42.2)	47.7	2.0	1.3
<i>Qff</i>	(0.4)	1.2	17.4	(14.4)	(2.5)	(1.1)
<i>Qb</i>	(7.5)	(1.2)	(45.5)	38.3	13.3	2.8
<i>Ql</i>	1.0	(1.2)	(54.3)	(12.7)	(3.0)	70.3
<i>Qsh</i>	3.0	0.7	(15.1)	13.6	(1.1)	(1.1)
<i>Qph</i>	41.5	(1.2)	(55.5)	(17.0)	26.5	5.7
<i>Qfp</i>	(3.7)	(1.2)	(36.5)	(9.2)	16.0	34.6
<i>Qmi</i>	3.6	(1.2)	(28.2)	27.0	0.0	(1.1)
<i>Qe</i>	(8.5)	(1.2)	(55.5)	36.1	30.3	(1.1)
<i>Qpr</i>	(8.5)	(1.2)	11.2	2.7	(3.0)	(1.1)
<i>Qn</i>	91.5	(1.2)	(55.5)	(30.6)	(3.0)	(1.1)

- *Quercus alba*
White Oak

28 % of measured oaks



- *Q. velutina*
Black Oak

25 % of measured oaks

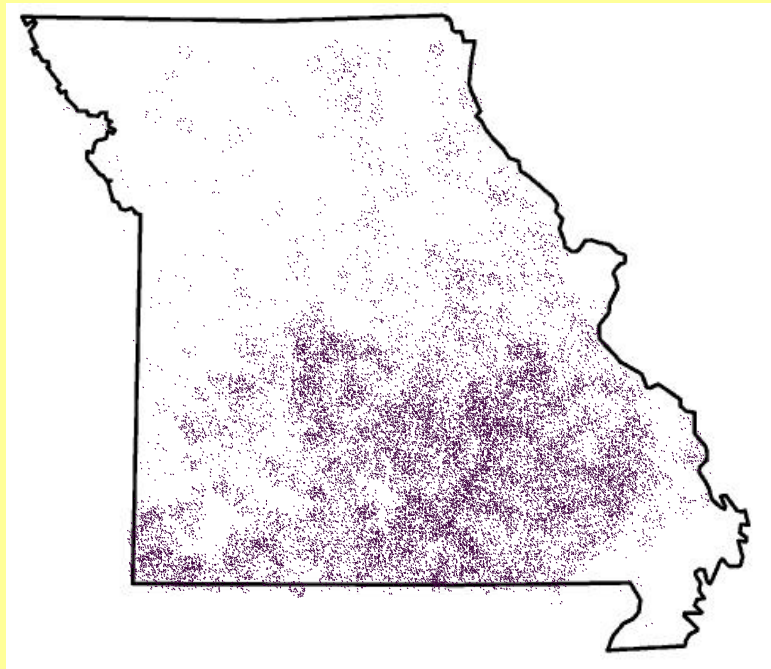


Figure I.4. Distribution of *Quercus alba* and *Q. velutina* in Missouri (FIA 1989). Points indicate occurrence of measurement trees on plots. Noise has been added to separate points per plot.

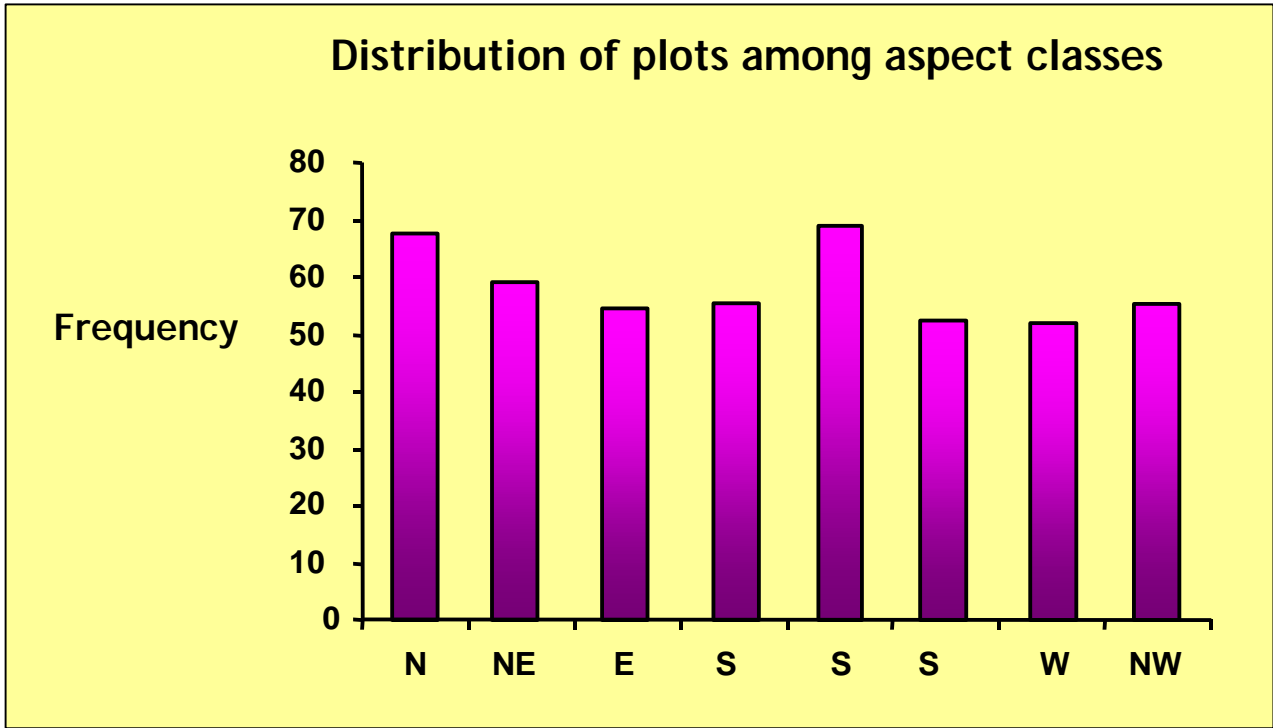


Figure I. 5. Distribution of FIA sample plots (1989) among aspect classes.

Table I.5: Distribution of FIA timberland plots among physiographic land classes (all trees > 1 inch) (FIA 1989).

Physiographic Class	Code	N	Percent of Total
Xeric	3	58	1.2%
Xeromesic	4	2595	55.5%
Mesic	5	1431	30.6%
Hydromesic	6	142	3.0%
Hydric	7	51	1.1%
Unknown	0	396	8.5%
Total		4673	

There is a minor preference of *Q. alba* for the mesic conditions of northerly aspects (Table I.6; Figure I.6).

As with all white oaks, *Q. alba* flowers emerge in early spring between March and May, pollination occurs, and if successful, the ovules are fertilized and acorns mature in late-summer and fall from the canopy in September and October of the same year (Rogers 1990). Good acorn crops occur at 4 to 10 year intervals and trees begin bearing after about 50 years although open-grown trees can begin producing acorns after 20 years. Trees at maturity reach 24 to 30 meters in height and 90 to 120 cm in diameter (DBH). The species typically is slower growing than oaks of similar stature in the red oak group (*Q. coccinea*, *Q. rubra*, and *Q. velutina*) but faster than the chestnut oak, *Q. prinus*.

I.3.2.2. *Quercus velutina* –

In the U.S., *Q. velutina* (black oak) is found throughout the East from eastern Kansas and Texas, south of south-east Minnesota and southern Maine, and north of southern Georgia and the Florida panhandle (Sander 1990). Across its range, the species does best on mid- to lower-slopes with a moderate mean temperature (13° C) and 1000 to 1300 mm of precipitation. At the western limits of its range, *Q. velutina* is most commonly found on north facing slopes due to increased moisture availability and at its northerly limits on ridges and lower south and west slopes due to more favorable temperatures.

In Missouri, *Q. velutina* is the second most numerous oak species with about 700 million trees (Table I.1) and is more commonly found in the southern half of the state (Figure I.7). On the MOFEP sites, *Q. velutina* is not only the most common oak species,

Table I.6: Distribution of oaks on FIA timberland plots among aspect classes (all trees > 1 inch) See table I.1 for species acronym key. .See table I.1 for the species acronym key (FIA 1989) .

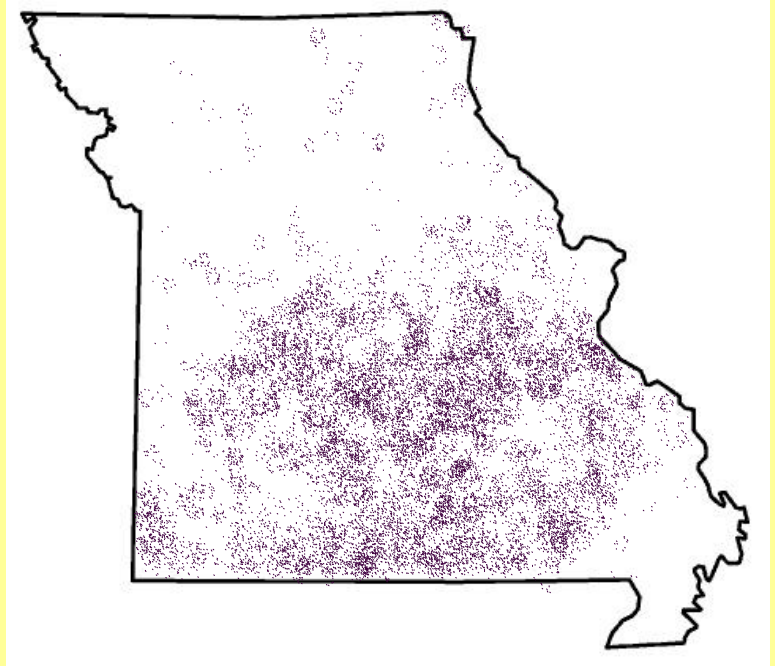
	Aspect Category								Number of Trees
	E	N	NE	NW	S	SE	SW	W	
<i>Qv</i>	12.0%	14.7%	12.9%	12.2%	14.7%	12.0%	10.9%	10.8%	22724
<i>Qa</i>	11.9%	17.2%	15.9%	14.4%	11.5%	9.7%	8.5%	10.9%	22587
<i>Qst</i>	11.9%	10.0%	10.4%	8.8%	17.5%	15.5%	14.5%	11.3%	17858
<i>Qmr</i>	10.5%	10.1%	8.7%	8.2%	21.4%	13.6%	16.4%	11.2%	5327
<i>Qc</i>	11.1%	15.3%	10.9%	12.3%	17.5%	10.3%	10.0%	12.7%	5079
<i>Qr</i>	10.9%	20.5%	16.5%	14.2%	9.0%	9.9%	7.4%	11.6%	3830
<i>Qmu</i>	11.2%	14.9%	9.1%	10.0%	15.3%	8.7%	14.9%	15.8%	1947
<i>Qi</i>	10.6%	15.4%	11.4%	8.1%	17.8%	11.9%	12.1%	12.5%	1367
<i>Qpa</i>	15.6%	16.3%	10.6%	5.2%	18.2%	13.3%	11.5%	9.3%	803
<i>Qma</i>	13.3%	21.9%	13.0%	11.5%	10.9%	6.3%	12.6%	10.6%	540
<i>Qff</i>	6.0%	16.4%	8.8%	7.9%	18.6%	17.9%	7.9%	16.7%	420
<i>Qb</i>	11.4%	16.3%	10.2%	10.0%	19.2%	11.2%	10.0%	11.7%	411
<i>Ql</i>	4.8%	16.7%	1.2%	17.9%	42.9%	0.0%	8.3%	8.3%	84
<i>Qsh</i>	7.7%	11.5%	5.8%	34.6%	7.7%	7.7%	19.2%	5.8%	52
<i>Qph</i>	0.0%	47.7%	34.1%	0.0%	11.4%	4.5%	2.3%	0.0%	44
<i>Qfp</i>	4.8%	7.1%	23.8%	7.1%	2.4%	45.2%	2.4%	7.1%	42
<i>Qmi</i>	21.2%	9.1%	3.0%	12.1%	9.1%	0.0%	6.1%	39.4%	33
<i>Qe</i>	33.3%	0.0%	0.0%	0.0%	66.7%	0.0%	0.0%	0.0%	3
<i>Qpr</i>	33.3%	0.0%	0.0%	33.3%	0.0%	33.3%	0.0%	0.0%	3
<i>Qn</i>	0.0%	0.0%	0.0%	0.0%	100.0%	0.0%	0.0%	0.0%	1
Plot Distr.	11.7%	17.5%	12.6%	11.9%	15.0%	11.8%	8.3%	11.1%	
Number of Trees Measured	9722	12045	10610	9713	12398	9930	9373	9364	

Table I.-6b: Distribution of oaks among aspect classes (all trees > 1 inch). These values indicate the difference between the observed distribution of trees among classes and the overall distribution of plots among plots. Negative values (in parentheses) indicate fewer trees than would be expected if evenly distributed, positive values indicate a greater number of trees per class than would be expected. See table I.1 for the species acronym key (FIA 1989).

Aspect Category								
	E	N	NE	NW	S	SE	SW	W
<i>Qv</i>	0.3	(2.9)	0.2	0.2	(0.3)	0.1	2.6	(0.3)
<i>Qa</i>	0.1	(0.3)	3.3	2.5	(3.5)	(2.1)	0.3	(0.2)
<i>Qst</i>	0.2	(7.5)	(2.3)	(3.2)	2.6	3.7	6.2	0.2
<i>Qmr</i>	(1.3)	(7.5)	(3.9)	(3.7)	6.4	1.8	8.1	0.1
<i>Qc</i>	(0.6)	(2.2)	(1.8)	0.4	2.5	(1.6)	1.7	1.6
<i>Qr</i>	(0.9)	3.0	3.9	2.2	(6.0)	(1.9)	(0.8)	0.5
<i>Qmu</i>	(0.5)	(2.6)	(3.5)	(2.0)	0.3	(3.1)	6.6	4.7
<i>Qi</i>	(1.1)	(2.1)	(1.2)	(3.8)	2.9	0.1	3.9	1.4
<i>Qpa</i>	3.8	(1.2)	(2.0)	(6.7)	3.2	1.5	3.2	(1.7)
<i>Qma</i>	1.6	4.3	0.3	(0.4)	(4.1)	(5.5)	4.3	(0.5)
<i>Qff</i>	(5.8)	(1.1)	(3.8)	(4.1)	3.6	6.0	(0.4)	5.6
<i>Qb</i>	(0.3)	(1.2)	(2.4)	(2.0)	4.2	(0.6)	1.7	0.6
<i>Ql</i>	(7.0)	(0.9)	(11.4)	5.9	27.9	(11.8)	0.0	(2.7)
<i>Qsh</i>	(4.0)	(6.0)	(6.9)	22.7	(7.3)	(4.1)	10.9	(5.3)
<i>Qph</i>	(11.7)	30.2	21.5	(11.9)	(3.6)	(7.3)	(6.0)	(11.1)
<i>Qfp</i>	(7.0)	(10.4)	11.2	(4.8)	(12.6)	33.4	(5.9)	(3.9)
<i>Qmi</i>	9.5	(8.4)	(9.6)	0.2	(5.9)	(11.8)	(2.2)	28.3
<i>Qe</i>	21.6	(17.5)	(12.6)	(11.9)	51.7	(11.8)	(8.3)	(11.1)
<i>Qpr</i>	21.6	(17.5)	(12.6)	21.4	(15.0)	21.5	(8.3)	(11.1)
<i>Qn</i>	(11.7)	(17.5)	(12.6)	(11.9)	85.0	(11.8)	(8.3)	(11.1)

- ***Quercus stellata***
Post Oak

24 % of measured oaks



- ***Q. marilandica***
Blackjack Oak

8 % of measured oaks

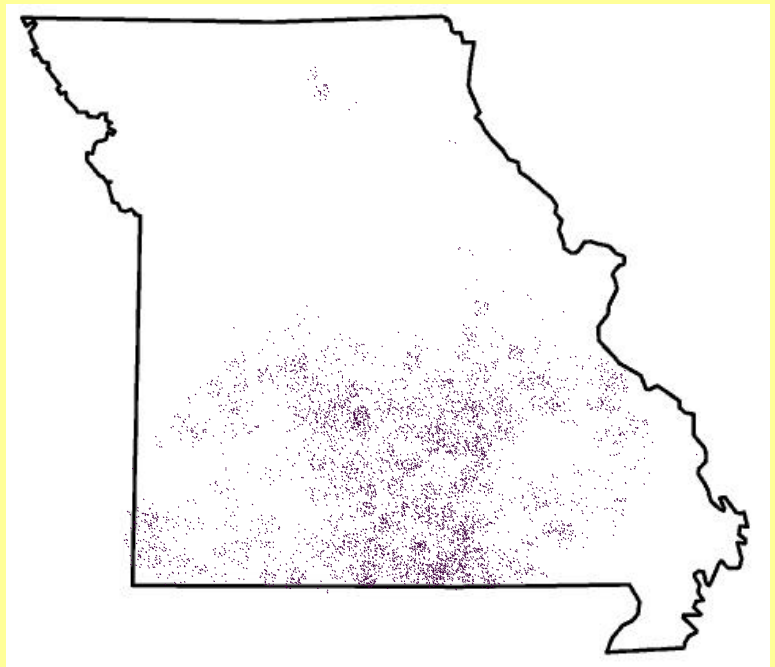


Figure I.7 Distribution of *Q. stellata* and *Q. marilandica* in Missouri (FIA 1989). Points indicate occurrence of measurement trees on plots. Noise has been added to separate points per plot.

but is the most common tree species comprising about 23 percent of all sample trees greater than 12.7 cm (5 inches) in DBH (Table I.3). Most of the trees of this species are found on xeromesic (69 percent) or mesic (19 percent) sites (Table I.4) and are about equally distributed among aspect classes (Table I.6; Figure I.6).

Trees of *Q. velutina* begin producing acorns after about 20 years and maximize acorn production between 40 and 75 years (Sander 1990). Good seed crops occur at 2 to 3 year intervals. Trees mature at about 100 year and may typically live between 150 and 200 years reaching 18 to 24 m (60 to 80 feet) in height and 60 to 90 cm (24 to 36 inches) in diameter. The rate of growth is faster than that of the white oaks but slower than that of *Q. rubra*.

I.3.2.3. *Quercus stellata* –

The range of post oak (*Q. stellata*) in the U.S. extends from southern New York to the northern half of Florida, west to mid-central Texas and Oklahoma and as far north as mid- Missouri, Illinois, Indiana, and Ohio (Stransky 1990). This species is a slow growing oak of the white oak group, typically found on rocky outcrops, ridges and upper slopes with west and southwest exposures. In number, *Q. stellata* trees are about 24 percent of the oaks or about 9 percent of all trees in Missouri. While found throughout the state, the species is sparsely distributed in the northwest quarter. In the Ozarks, post oaks are only about 6 percent of the inventoried oaks on the MOFEP sites. *Q. stellata* is tolerant of dry sites. It is more abundant on south and southwest slopes in Missouri (Figure I.6; Table I.6) and is found at a relatively higher rate (2.36 percent of trees) on xeric plots (Table I.4). In the southeast extent of its overall range, *Q. stellata* can reach

15 to 18 m in height (50 to 60 feet) and 30 to 60 cm in diameter (12 – 24 in.). At the western limits of the range, *Q. stellata* reaches a lower maximum height (9 to 12 m) and a smaller maximum diameter range (38 to 46 cm). It has a lower growth rate than most oaks.

Post oak trees begin flowering at about age 25 and produce acorn crops at 2 to 3 year intervals. In a study of *Q. stellata* spanning 18 years in Texas and Louisiana, the range in acorn production among 736 trees was from 0.07 lbs per year in 1962 to 9.7 lbs per tree in 1965 (Goodrum et al. 1971).

I.3.2.4. Quercus marilandica –

Blackjack oak is a species often found on soils of low fertility. In number it comprises about 8 percent of the oaks in Missouri and about 1.6 percent of the oaks on the Ozark MOFEP sites. It has a slightly higher than average presence on sites with a southern aspect and 74 percent of the estimated 223 million trees are on xeromesic sites. The species is rarely found in the northern half of the Missouri. Trees may reach 9 to 12 m, are slow growing and relatively short lived. The species is resistant to fire by virtue of its thick bark. Since this species has little commercial value, it has not been studied intensively but perhaps due to branching along the entire stem, the species is considered important for providing cover, habitat, and food for wildlife.

I.3.2.5. Quercus coccinea –

Scarlet oak is found in the eastern U.S. as a small understory or edge tree in southern Maine and increasing along in importance along the Appalachian mountains

south to Pennsylvania and Virginia, west from central North Carolina and northern Georgia to Tennessee, Kentucky, southern Illinois, and Indiana (Johnson 1990). Scarlet oak extends beyond that contiguous range to be an important component of the forest of the Ozarks and south-western region of Missouri. While *Q. coccinea* comprises only 5.6 percent of the oaks in Missouri, it is about 21 percent of the oaks on the MOFEP sites. Figure I.8e shows the relatively high concentration in that region. Although the species is almost evenly distributed among the aspect classes (Table I.6), the majority of the trees come from sites that are limited to a small region where conditions are moderate in terms of stress.

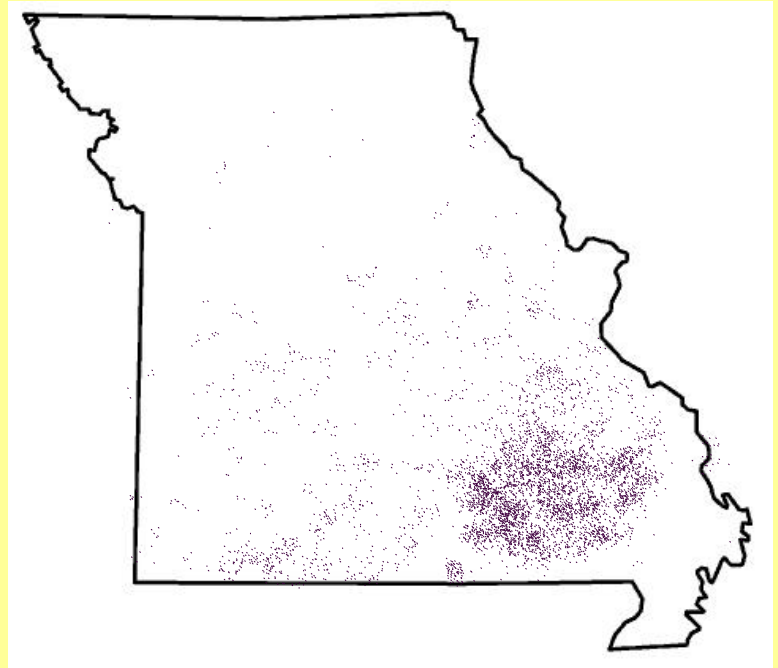
Good acorn crops may be expected at 3-5 year intervals beginning at about 20 years of age and maximizing production at over 50 years. It is a relatively poor acorn producer, with one study reporting only 25 acorns per square meter of crown area in comparison to 70 and 75 acorns m⁻² for *Q. velutina* and *Q. alba*, respectively.

I.3.2.6. Quercus rubra –

Northern red oak (*Q. rubra*) is found throughout the eastern U.S. north of the Georgia Mountains and Arkansas-Missouri and east of Minnesota (Sander 1990). The estimated 89 million trees found in Missouri comprise 3.8 percent of the oaks and are evenly distributed throughout the state (Figure I.8). There is a slight increase in presence in the central portion of the state; in fact, of over 96,000 trees inventoried on the MOFEP sites located in the south-central region of the state, only 5 were *Q. rubra*. There is a pattern of higher preference for northern aspects (Figure I.8) in Missouri.

e) *Quercus coccinea*
Scarlet Oak

6 % of measured
oaks



f) *Querrcus rubra*
Northern Red Oak

3 % of measured
oaks

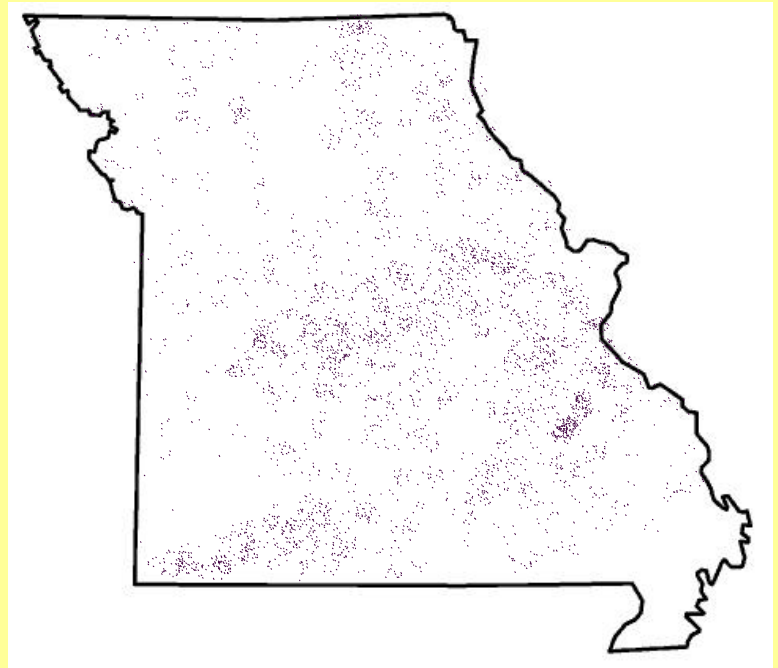


Figure I.8 Distribution of *Q. coccinea* and *Q. rubra* in Missouri (FIA 1989). Points indicate occurrence of measurement trees on plots. Noise has been added to separate points per plot.

This species, like many oak species begins producing acorns after about 25 years, but is not an abundant producer until about 50 years of age. Good crops may occur at 2 to 5 year intervals.

I.3.2.7. Quercus palustris –

The relatively low occurrence of pin oak in Missouri (0.74 percent of oaks), is offset by the importance of the species in providing hard mast on a relatively frequent basis for wildlife, waterfowl in particular. The range of pin oak extends from the mid-Atlantic States to southern Michigan, Illinois, southeast Iowa, and lower elevations of Missouri and Arkansas, Kentucky and Tennessee (McQuilken, 1990). The species is found on level to nearly level sites and can withstand periodic flooding. About 29 percent of the FIA inventoried trees were on hydromesic and hydric sites (Table I.4). No trees of this species were on the MOFEP sample plots in the Ozarks.

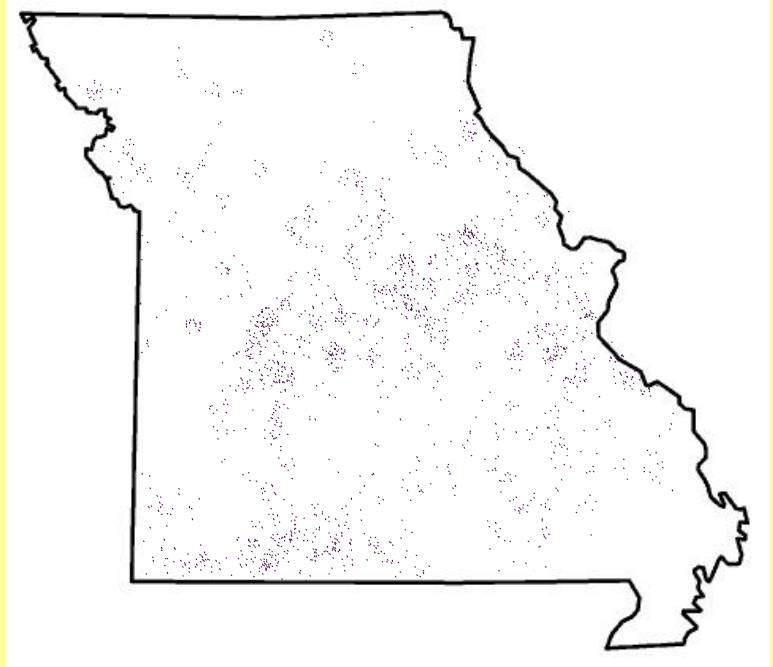
Among oaks, pin oak grows relatively rapidly and is capable of reaching 30 cm in diameter and 20 m tall in 30 years in southern Missouri (McQuilken, 1990). Acorn production begins at about 20 years; however, it is a relatively short-lived tree reaching physiological maturity at 80 to 100 years. An “old-growth” pin oak stand in Kentucky was found to be about 140 years in age. The species is considered to be intolerant and is usually found in even-aged stands.

I.3.3 Previous studies of acorn production

One of the confounding issues in characterizing acorn production from the available literature is the wide range of units of measure. In part, they are dictated by

Quercus muehlenbergii
Chinkapin Oak

2.4 % of measured
oaks



- ***Quercus imbricaria***
Shingle Oak

1.9 % of measured
oaks

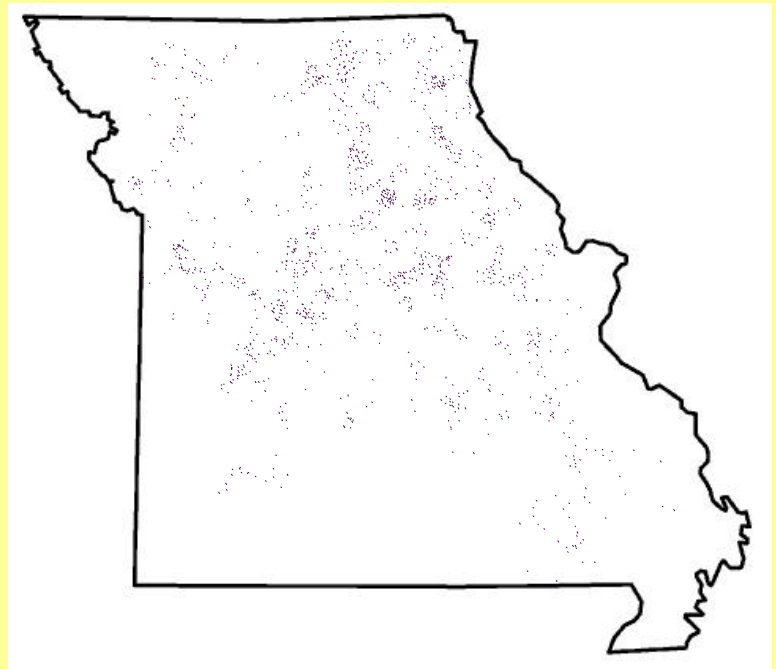
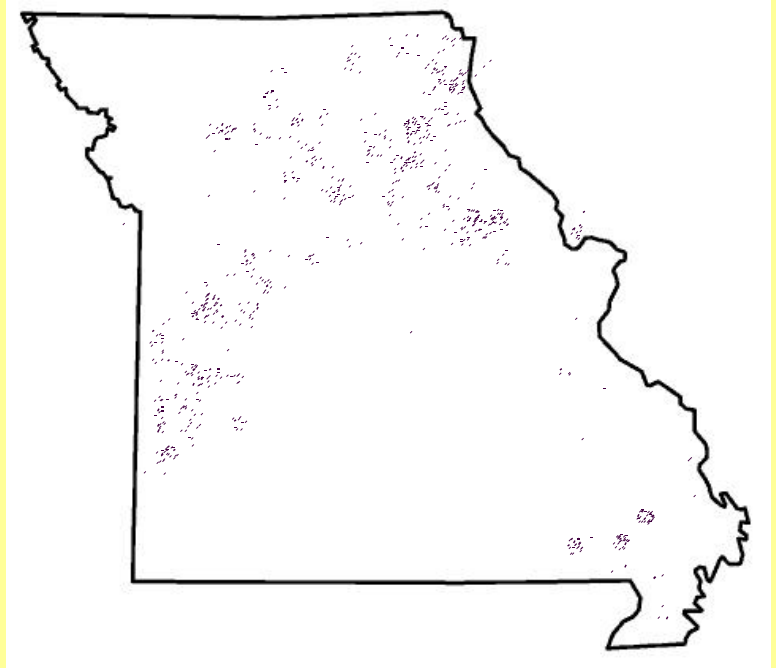


Figure I.9 Distribution of *Q. muehlenbergii* and *Q. imbricaria* in Missouri (FIA 1989). Points indicate occurrence of measurement trees on plots. Noise has been added to separate points per plot.

- *Quercus palustris*
Pin Oak

0.74 % of measured oaks



- *Quercus falcata*
Southern Red Oak

0.50 % of measured oaks

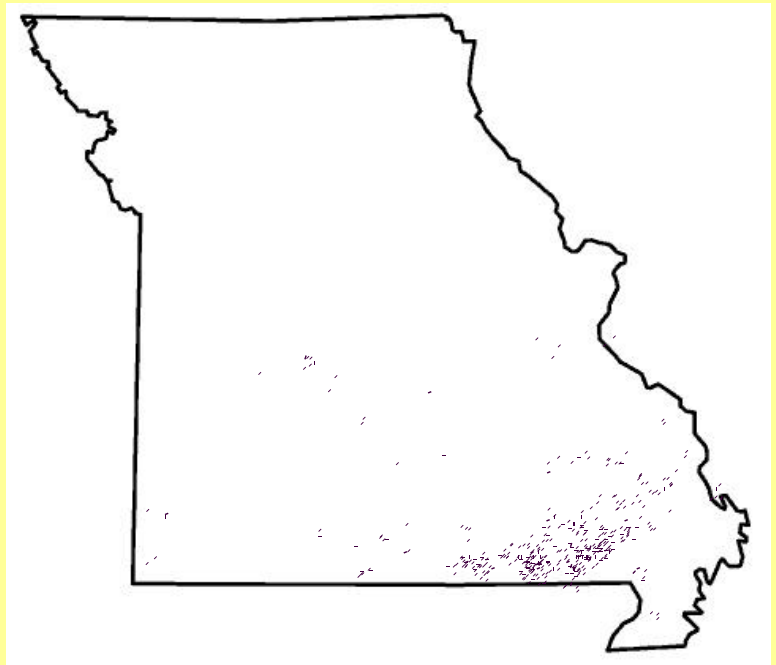


Figure I.10 Distribution of *Q. palustris* and *Q. falcata* in Missouri (FIA 1989). Points indicate occurrence of measurement trees on plots. Noise has been added to separate points per plot.

sample design and in part by the objectives of the authors. Typical units include either number of acorns or mass of acorns by tree, per unit land area, per unit tree diameter, or per unit stand basal area. In addition, mass can be expressed on a fresh weight basis or dry-weight basis and number can refer to acorn-cap counts or whole acorns. The potential viability of acorns is of interest to those studying forest regeneration, thus some studies report only sound, well-developed acorns. When observing a large number of sample trees, Koenig (1991) used an index that relates the number of acorns counted in 15 seconds. The following summaries are left, for the most part, in original units. Section II deals with translation of these values to index formulation.

I.3.3.1 Flowering

A study in Kentucky during 1962 and 1963 reports that only 1.3 and 3.5 percent of the pistillate (female) flowers developed into acorns (Williamson 1966). About 90 percent of all abscissions occurred between the between April 30th and July 15th. The specific stage of development during which abscission occurred is shown in Table I.7. Each year displayed a similar pattern, although in 1962 a much higher number of flowers failed during pollination. Feret (1982) reported 70 % failure rate of *Q. alba* flowers over a period of 4 years. A late spring freeze (4.4 °C, May 10th) in southeast Ohio resulted in a complete loss of *Q. alba* flowers for 1966 and a loss of most developing *Q. velutina* embryos (Nixon and McClain 1969). Sharp and Sprague (1967) reported that during the period between 1949 and 1962, spring temperature regimes affected acorn yields in Pennsylvania. They hypothesized that a warm April followed by a cool May delayed pollen dispersal to coincide with receptivity of pistillate flowers. Conversely, a cool

Table I.7: The percentage of flowers abscising (failing) during stages of development for a two year study in Kentucky (Williamson 1966).

Stage	1962	1963
Pollination	56.0%	28.0%
Ovule development	10.6%	38.0%
Fertilization	15.8%	18.1%
Embryo	16.7%	10.5%
Percent of total flowers producing mature acorns	1.3%	3.5%

April, and a warm May led to poor acorn yields. In comparison to spring temperatures, wind, precipitation, and relative humidity had little effect on acorn yield. In 1955, dry winds desiccated catkins (staminate flowers) resulting in premature pollen shed. In 1956 a freeze event in May led to crop failure, but a similar freeze event the following year did not affect the acorn crop due to radiative reflection by cloud cover. Cecich (1992) noted that while one can predict the number of acorns from developing, fertilized flowers, one cannot accurately predict the number of successful flowers a tree will produce.

1.3.3.2 Masting and site characteristics

Gysel (1957) monitored acorn production from 1953 to 1956 on good, moderate, and poor oak sites. Species and size composition differed among sites and these differences may have contributed to apparent differences in acorn production (Figure I.11). Auchmoody (1993) measured acorn production for four years in northwest Pennsylvania at 21 stands that were similar in diameter and species structure. In three of the years, spring freezes destroyed most of the potential acorn production. Not all sites were affected each year, suggesting that small differences in elevation or location may allow some sites to maintain flowers. VanGilder (1997), in reporting the results of pre-treatment sampling for monitoring 130 plots from 4 ecological land-type groups, noted that ridge plots produced the largest number of acorns and that plots located along streams (lowland) produced the least.

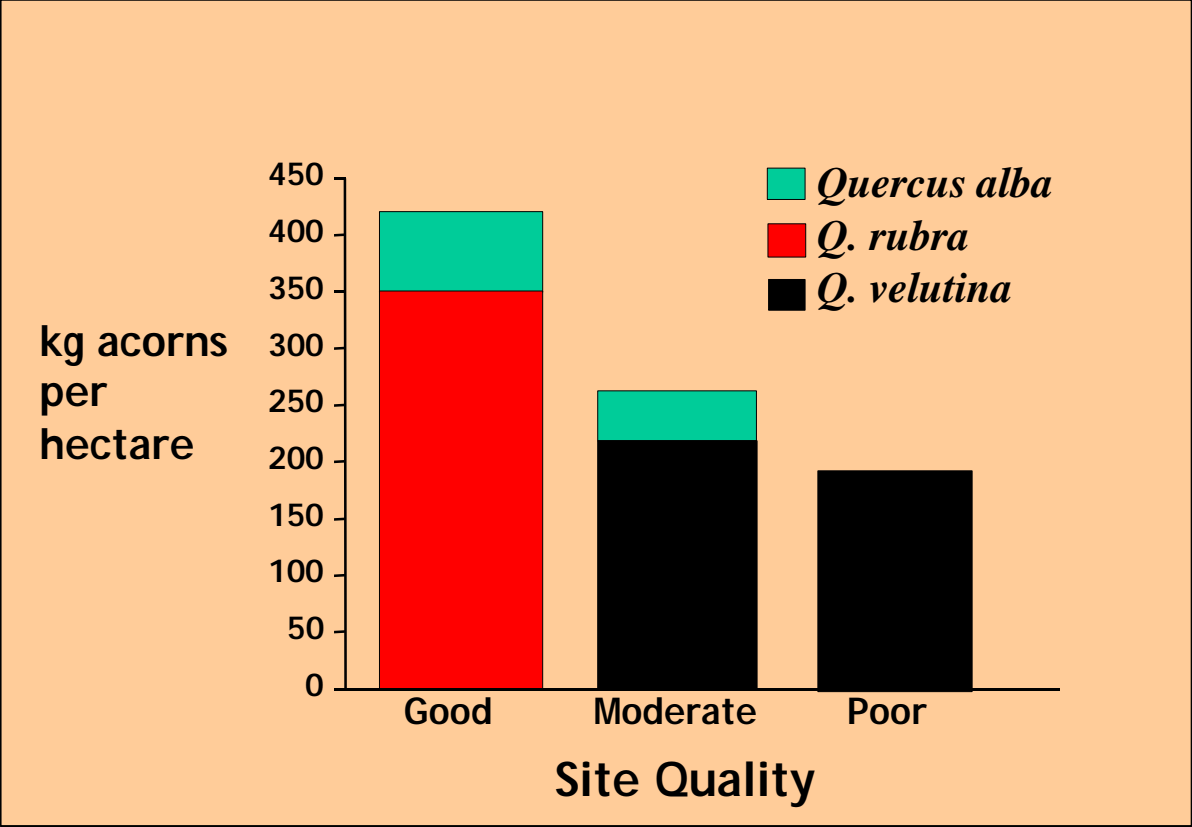


Figure I.11. Acorn production as a function of site quality from 1953 to 1956 in Michigan (Gysel 1957).

I.3.3.3 Tree and stand characteristics and masting

In a study of 765 trees across many sites in the Southern Appalachians from 1993 to 1997, Greenberg (2000) noted that trees less than 25 cm in diameter (approx. 10 inches) produced few acorns. *Q. rubra* and *Q. alba* produced significantly more acorns than other species. Only 20 percent of *Q. prinus*, 29 percent of *Q. velutina*, 33 percent of *Q. coccinea*, 31 percent of *Q. alba*, and 46 percent of *Q. rubra* trees were consistently good producers of acorns. The relationship between acorn production and diameter probably reflects that the relationship between diameter and crown dimensions. Krajicek *et al.* (1961) fit a model of crown area using measured diameter with good predictive ability. Goodrum (1971) noted that about 30 percent of *Q. alba* trees in the 8 and 10-inch diameter classes were producing acorns whereas 90 percent in the 16 and 18-inch diameter class were producing acorns. A similar pattern exists for *Q. stellata* (Figure I.12). Goodrum noted that few trees less than 20 years old produced acorns (1971) and Dickson (1990) suggested that optimal acorn production occurred between tree ages of 50 and 125 years. Auchmoody *et al.* (1993), for the years of their study, suggested that in Pennsylvania, spring temperatures and freezing were more important determinants of acorn production than stand basal area or mean stand diameter. For their trees, acorn production increased with increasing mean diameter until about 35 cm, and thereafter did not increase. This could be related as much to changing stand species distributions as to individual tree performance, i.e.. smaller mean diameter may reflect a higher presence of non-oak species.

As related previously, tree diameter affects acorn production (Figure I.1). There is a remarkably similar relationship between two studies of *Q. alba* by Goodrum (1971)

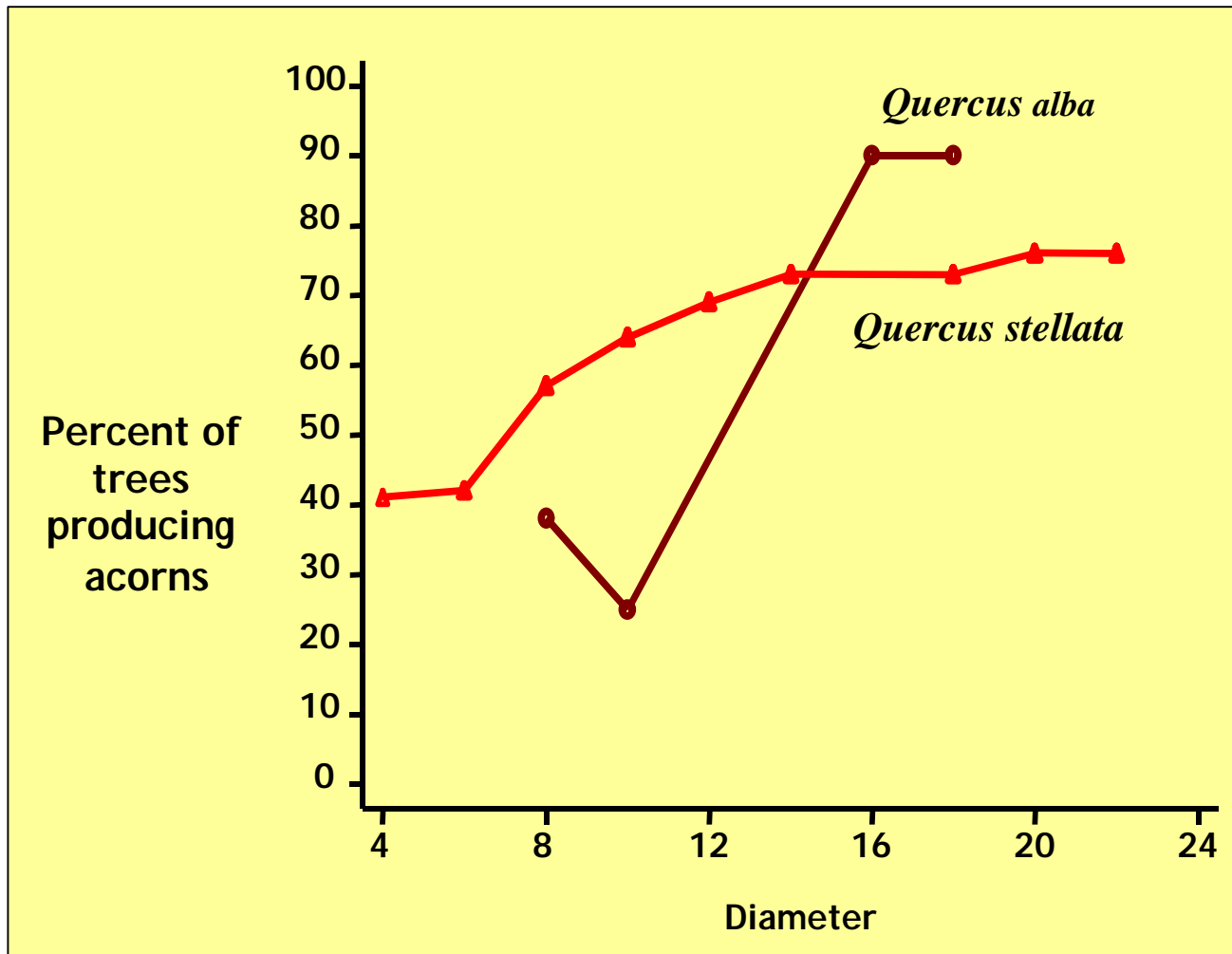


Figure I.12 The percentage of trees producing acorns for *Quercus alba* and *Q. stellata* (Goodrum 1971).

and Downs (1944). After conversion to equal units the slope of the Goodrum model of acorn production as a function of diameter is very close to that presented by Downs (Figure I.13). The difference in production per unit diameter (higher for the study in Texas and Louisiana) may be due to differences in site condition or differences in weather conditions during the two studies.

A study of four forest types in the southern Ozarks of Arkansas (Dickson 1990) between 1959 and 1977, where oak was a component of each type reported distinct differences in acorn production between the forest types (Figure I.14). These forest types express both the species composition and, indirectly, site quality. Thus the difference in acorn production is a combined expression of species distributions and site quality.

1.3.3.4 Silvicultural treatment and masting

Most studies have concluded that silvicultural management can increase acorn production. Sharp and Sprague (1967) suggested marking good acorn producers in mast years for preservation in a stand. Harlow and Eikum (1963) found that thinning a stand with a density of 150 to 75 trees per acre did not reduce acorn production for turkey oak (*Q. laevis* Walt.) in Florida. Trees for the residual stand were selected based on crown area and diameter, live crown length, and overall health. “Good” trees were 7 inches (18 cm) in diameter, had crown area greater than 200 square feet (19 m²), no apparent decay, and the height to first branches was less than 22 feet (6.7 m).

Minckler and McDermott (1960) investigating *Q. palustris* (pin oak) acorn production in southeastern Missouri from 1956 to 1959 recorded higher numbers of sound well-developed acorns on artificially flooded sites. In a subsequent publication,

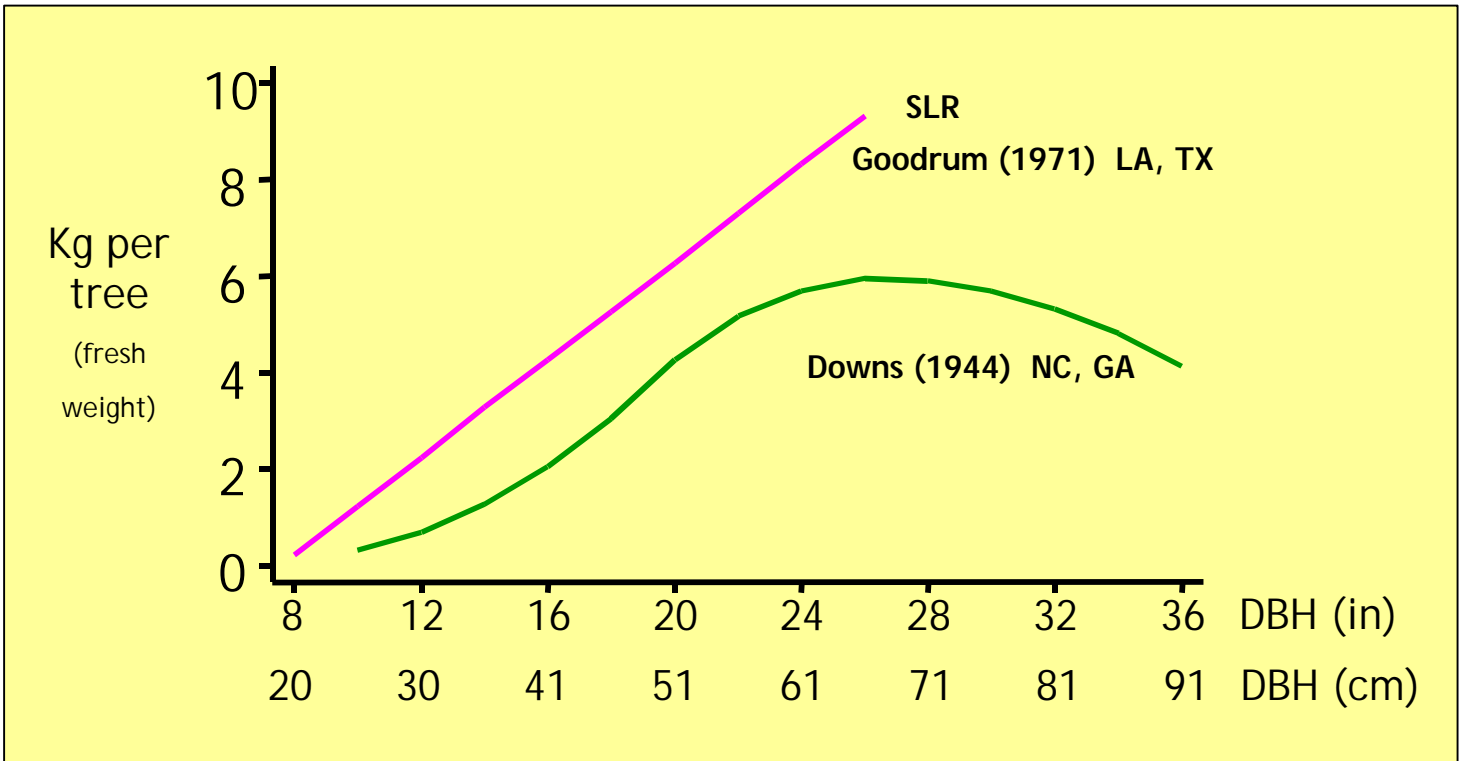


Figure I.13 Acorn production by diameter class from two studies of *Quercus alba*.

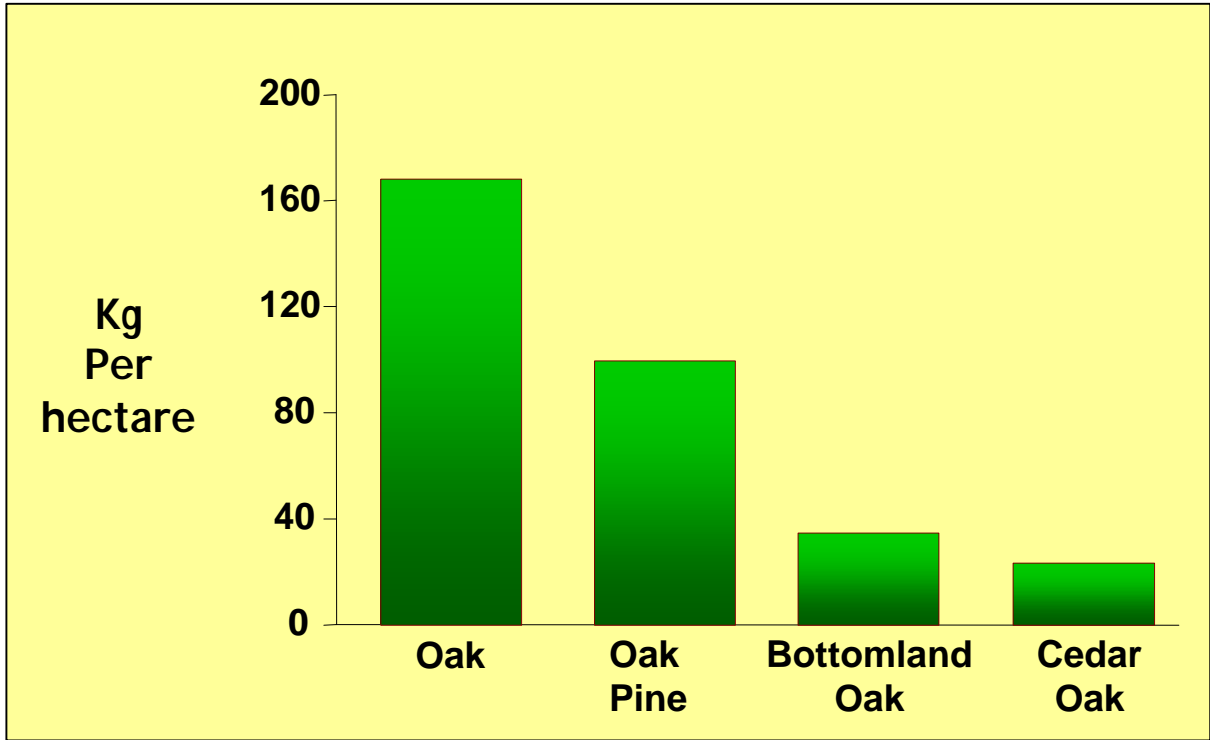


Figure I.14 Annual acorn production for four forest types in Arkansas (Dickson 1990).

Minckler and Janes (1965), found that acorn production followed the same pattern as the annual precipitation, i.e. an increase in precipitation (natural flooding) corresponded to increased acorn production.

Healy *et al.* (1997) reported that stands thinned to enhance acorn production produced more acorns than un-thinned stands. The un-thinned stand had about 1100 trees per hectare and the thinned stand 724 trees per hectare. Both stands had about 65 oak trees per hectare greater than 30 cm in diameter. However, the thinned stand had only 48 oak trees between 15 and 30 cm and the unthinned stand had 119 oak trees per hectare in this range. In a subsequent publication Healy *et al.* (1999) after adding 8 more years of data on these sites concluded that while the thinned stand did produce more acorns than the unthinned stand, the variation that occurred among years and among individual trees far exceeded the variation observed by the thinning treatment (Figure I.15). They estimated that by observing mast production for any three consecutive years, 87 percent of the good acorn producing trees could be identified. Farmer (1981), in a seed orchard study of *Q. alba* clones between 1975 and 1978, determined that similarity in acorn production existed among related trees; thus selection for good acorn production was possible. Drake (1991) attempted to improve acorn production through selective thinning in Pennsylvania and saw a slight increase in acorn production following the thinning treatment but did not think the resulting increase justified the expense (Figure I.16).

Stand age is one of the primary descriptors of sites for the LANDIS model. Unfortunately, there is a poor relationship between stand age and the parameter usually associated with acorn production, i.e. tree diameter, particularly for uneven aged stands (Loewenstein *et al.* 2000). Figure I.17 depicts an uneven-aged forest as a series of

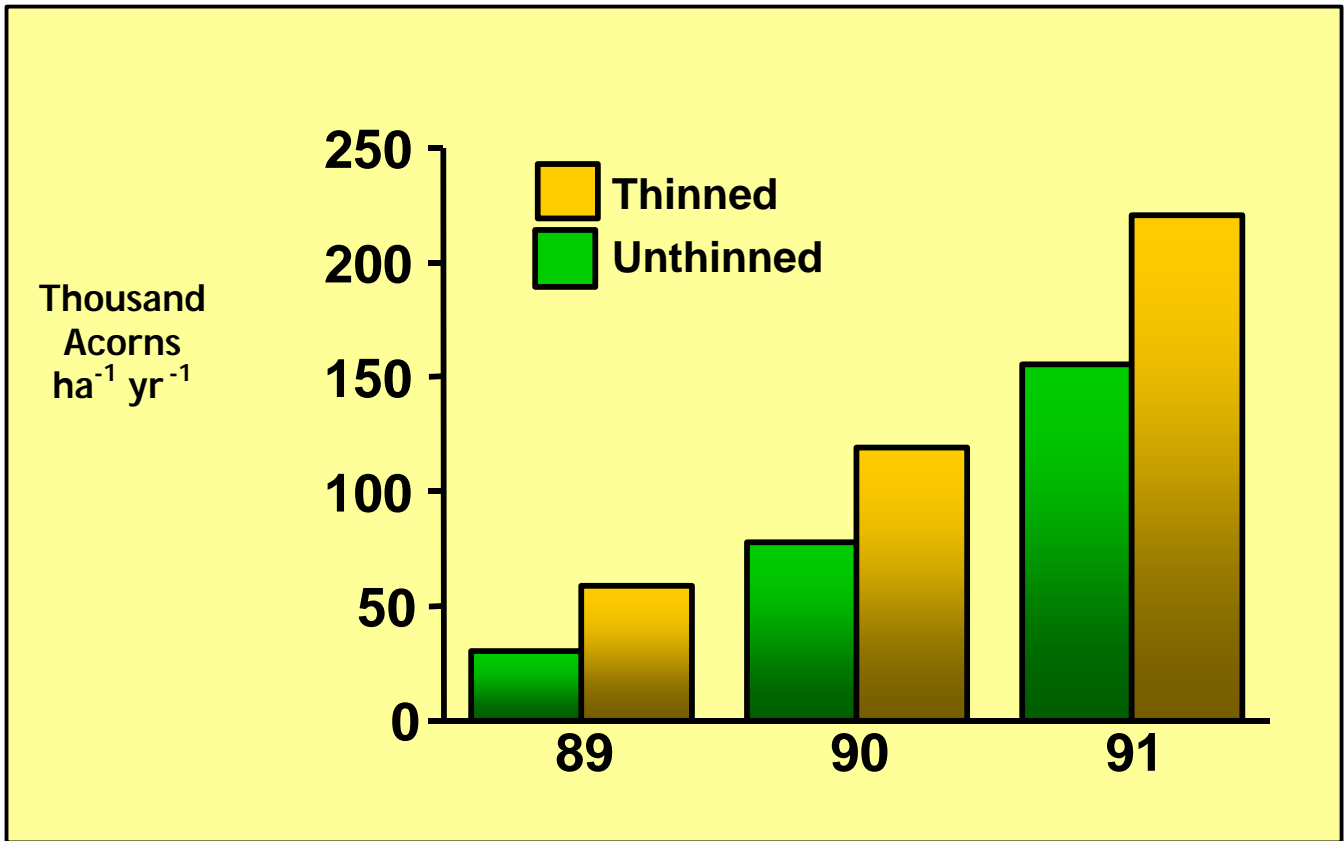


Figure I.15 Results of a thinning experiment in Massachusetts to increase acorn production (from Healy 1997).

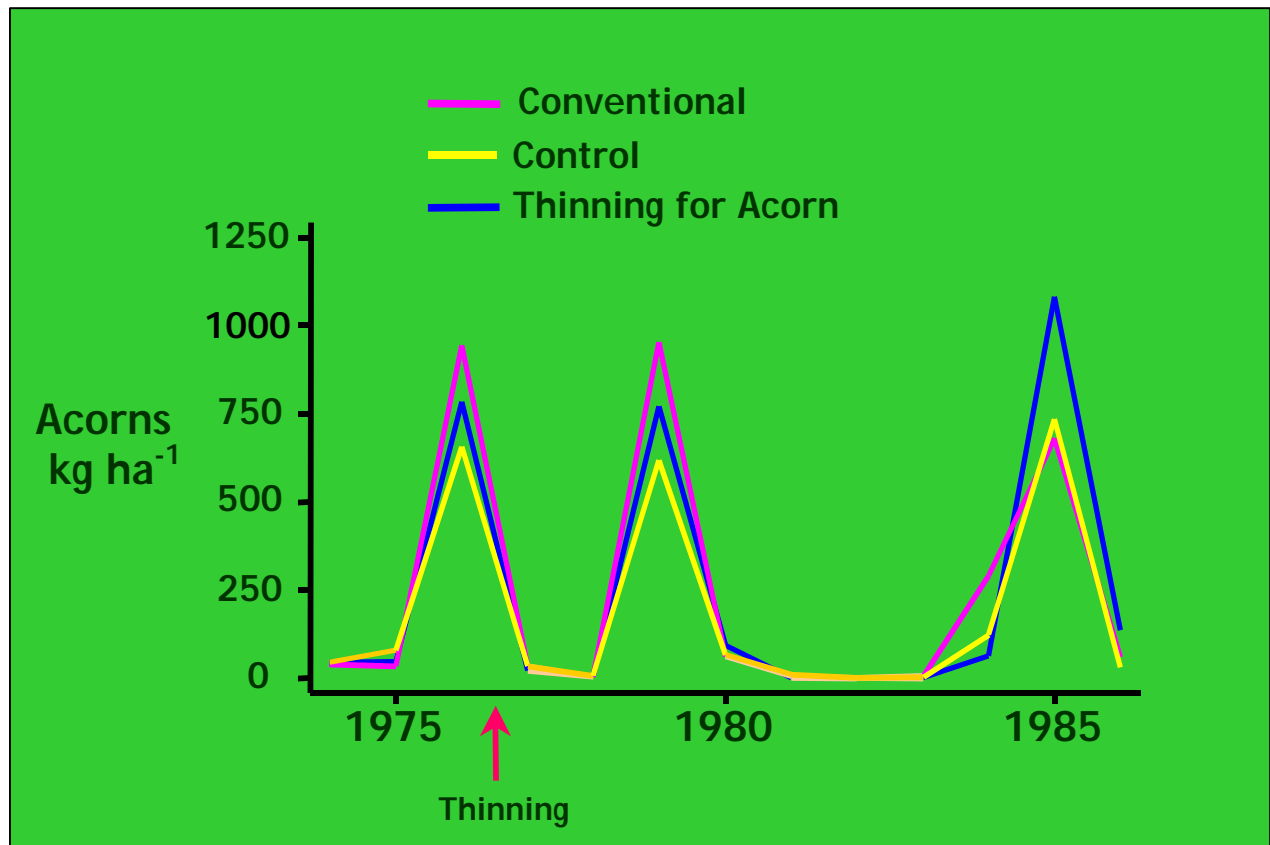
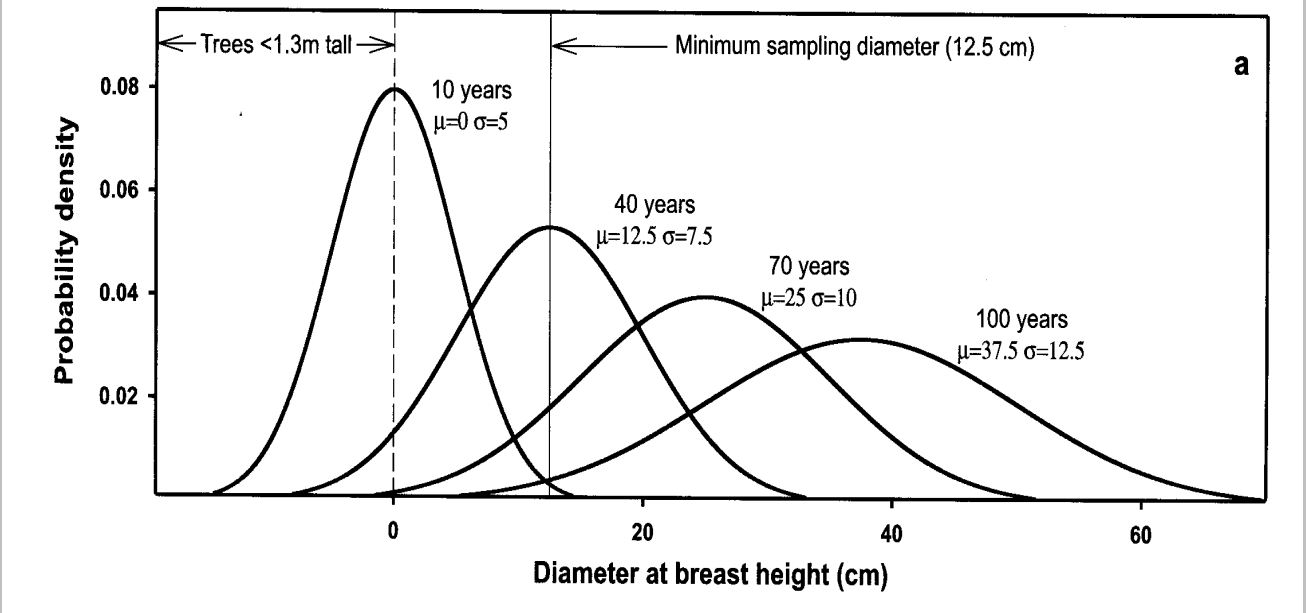


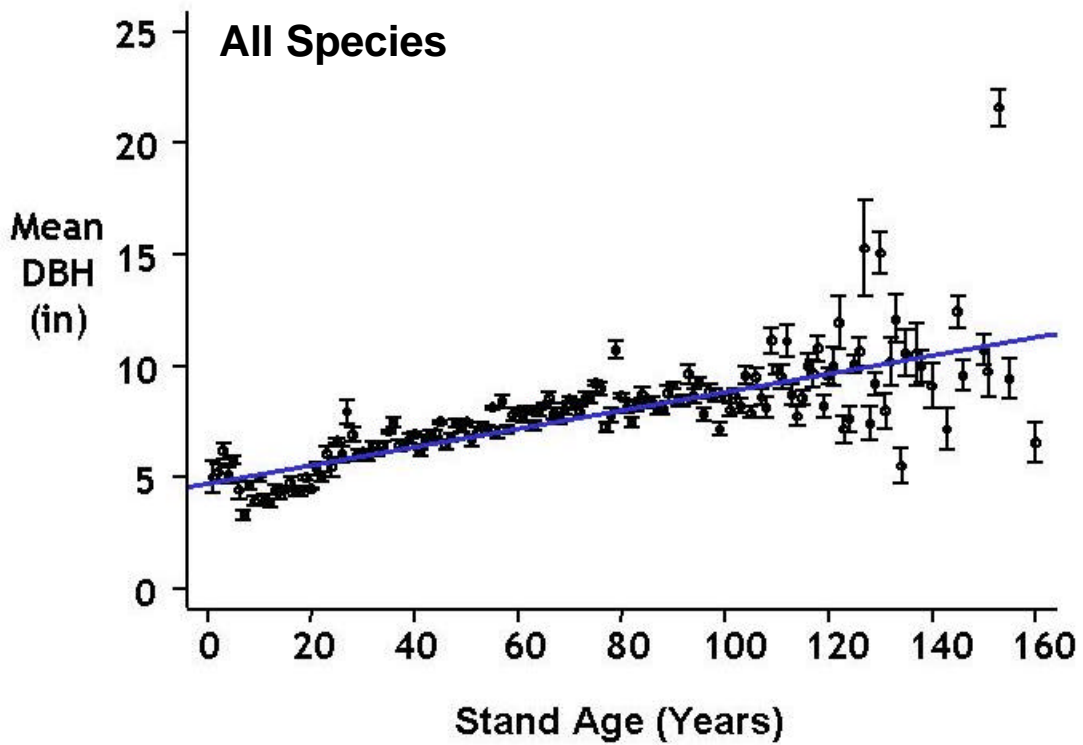
Figure I.16 Results of a thinning experiment in Pennsylvania to increase acorn production (Drake 1991).



normal distributions for cohorts of trees. The ability to accurately predict the diameters of trees on a particular site decreases with increasing stand age. However, generally speaking, forest trees must increase in diameter with age to attain and maintain a position in the canopy. If enough trees are sampled, models of the relationship can generate significant estimates of tree size. The 1989 FIA data provide an opportunity to examine the relationship at a much broader scale. Figures I.18 and I.19 show the mean diameter for each of the 146 stand ages recorded for the 1989 FIA inventory for all species and for oaks, respectively. Increased variation is apparent in stands greater than 100 years in age. While prediction of diameter from age is not appropriate at the tree or stand level, modeling at the landscape level where thousands of predictions are generated allows the opportunity to apply random number assignment from appropriately selected and specified distributions.

I.4 CONCLUSIONS

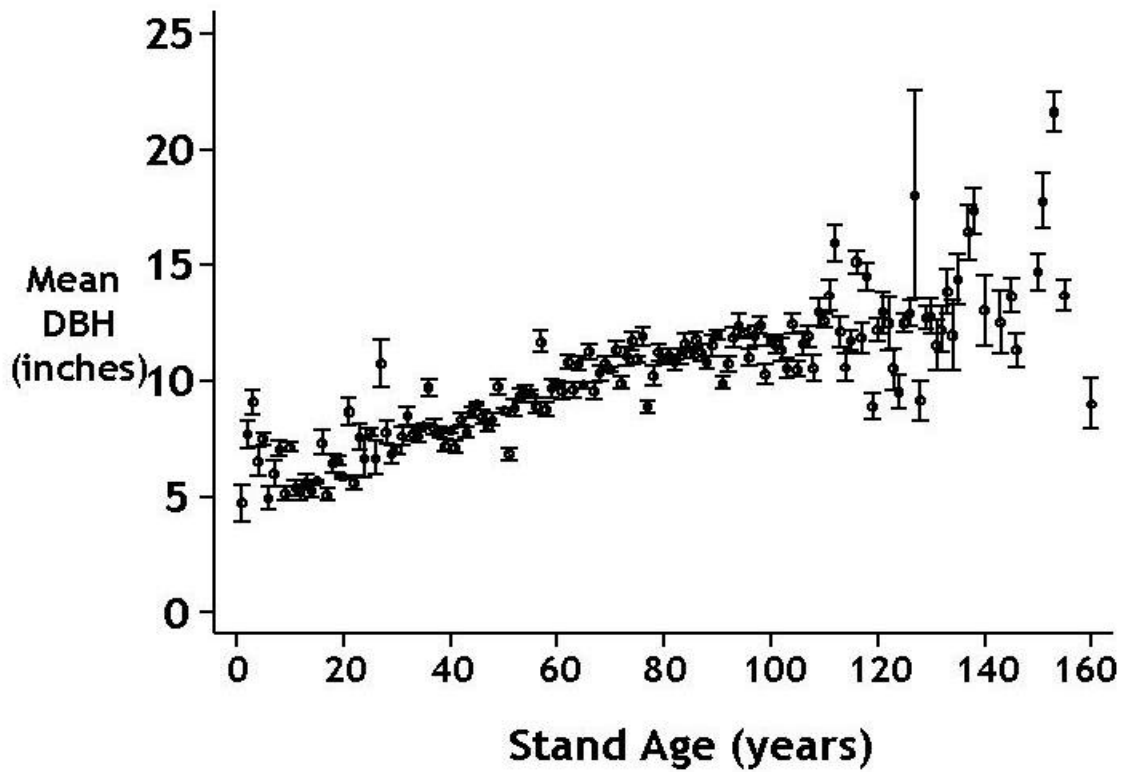
This section summarizes some of the available information pertinent to the objectives of this study. Given the variation in units of measure, the limitations and requirements of the LANDIS model, and variation in the perspectives of future users, *e.g.* management for wildlife or for regeneration of oak, I propose to generate a unitless index of potential mast production. For example, a stand that consists of all oak trees at the prime acorn producing age (75 to 125 years) on the best slope-position and aspect may be rated an index of 1000. This index could be adjusted for genetic variability in acorn production (reducing the index, *e.g.* to 600). However, as has been previously



$$DBH_{in} = .0409(\text{stand age}) + 4.85$$

$$P > |t| = .0005, R^2_{adj} = 0.564, n = 146$$

Figure I.18 The relationship between stand “representative” age and mean tree diameter ($\pm 1SE$) for all species on FIA plots in Missouri and a simple linear regression model describing the trend.



$$DBH_{in} = .0563(\text{stand age}) + 6.013$$

$$P > |t| = .0005, R^2_{adj} = 0.709, n = 146$$

Figure I.19 The relationship between stand “representative” age and mean tree diameter (± 1 SE) for oaks on FIA plots in Missouri and simple linear regression model describing the trend.

mentioned, intensive management through individual tree selection would likely decrease the amount of the reduction in the index. Deviations from optimal site conditions would provide justification for further deductions, e.g. mixed species distributions, bottomland sites etc. Once site and stand potential acorn production are indexed, annual variation can be factored using previous masting history as it relates to the availability of resources and the probability of successful pollination (e.g. the probability of favorable relative humidity during pollination). Since indices may not be of immediate apparent value to managers, the indices will be linked to units that are more meaningful. For example, the optimal production of acorns in units of mass may be set at 500 kg per hectare (e.g. Gysel 1957) whereas the optimal number of acorns may be set at 400,000 (Johnson 1975). Conversion factors are included in the concluding sections of this document.