A PERSPECTIVE ON *QUERCUS* LIFE HISTORY CHARACTERISTICS AND FOREST DISTURBANCE

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Abstract—Plant strategy theory suggests that life history characteristics reflect growth and reproductive adaptations to environmental disturbance. Species characteristics and abundance should correspond to predictions based on competitive ability and maximizing fitness in a given disturbance environment. A significant canonical correlation between oak growth attributes (height growth, xylem permeability, shade tolerance) and reproductive attributes (longevity, acorn weight, and the age to reproduction) based on published values indicates that the distribution of oak attributes among species is consistent with r and K selection theory. Growth and reproductive attributes were used to calculate an index reflecting the relative values of the r and K strategies of oak species. This index was used to examine changes in the dominance of oak species at nine sites in the Ozarks. Changes in oak species dominance and differences in their landscape distributions were consistent with predictions based on their r and K index values and estimates of forest disturbance.

INTRODUCTION

Plant strategy theory suggests that life history characteristics reflect growth and reproductive adaptations to population density, environmental disturbance, and stress (Grime 1979, Odum 1997). Species attributes and abundance should correspond to predictions based on competitive ability and maximizing fitness in a given disturbance environment. Thus, selection theory predicts that there should be correlations between growth and reproductive variables among species that are consistent with the species ability to remain competitive and maximize fitness in a given environment. The opposing strategies of r and K selective forces (MacArthur and Wilson 1967) have been used to explain persistence of species in given environments. Generally, r-strategists are those that have a high rate of reproduction and growth providing an advantage in acquiring resources made available through disturbance. A K-strategist has characteristics that allow it to more effectively compete for resources in communities that are near carrying capacity and where resources are predictable and relatively favorable.

Many consider r- and K-selection theory to be valid but an oversimplification (Crawley 1997) because it does not consider fitness attributes that are not influenced by population density. We use this theory because it lends itself to linear quantification among the species of a single genus whose member's life history strategies are similar in many respects. Grime (1979) classifies life history traits into three dimensions based on the overriding factors of stress and disturbance. Using this classification a competitor (C) plant species as one that persists in a low stress, low disturbance environment. A stress tolerator (S) exploits conditions of high stress and low disturbance; and a ruderal (R) represents a reproductively driven strategy and persists in low stress and high disturbance.

Oaks, members of the genus *Quercus,* represent the most important hardwood species group both ecologically and economically in North America. In addition to the 90 recognized species in North American (Flora Committee 1997) there are at least 70 hybrids in Northeastern Forest (Gleason and Cronquist 1991) and about 23 species in the Central Hardwood Region (Nixon 1997). As a group, oaks have wide ecological amplitude and can dominate highly varied environments. Oaks may all be classified as competitors or stress tolerators, *sensu* Grime (1979), but are not ruderal when compared to many tree species, e.g. *Populus, Salix, Robinia*. Differences in life history strategies should be especially clear within a genus such as *Quercus*, showing evolutionary divergence and speciation in response to environmental factors including disturbance and stress.

The objective of this study is to provide an understanding of how plant strategy theory can be quantified and evaluated based on numerous variables. The specific hypotheses are: (1) oak reproductive and growth characteristics are significantly correlated; (2) the distribution of these characteristics among species is consistent with r and K life history strategies. Furthermore, we intend to create a preliminary oak r and K Index for quantitative use and to use this index to examine and possibly predict relationships among life histories (the abundance of r and K attributes), disturbance frequency, oak species abundance, and basal area at nine sites in the Ozark Highlands of Missouri.

METHODS

We used data describing 13 oak species from the Central Hardwoods Region: white oak (*Quercus alba*), post oak (*Quercus stellata*), bur oak (*Quercus macrocarpa),* chinquapin oak (*Quercus muehlenbergii*), northern red oak (*Quercus rubra*), black oak (*Quercus velutina*), scarlet oak (*Quercus coccinea*), southern red oak (*Quercus falcate*), pin oak (*Quercus palustris*), blackjack oak (*Quercus marilandica*), swamp white oak (*Quercus bicolor*), overcup oak (*Quercus lyrata*), and nuttal oak (*Quercus texana*)*.* Variables and sources are listed in table 1. Only species with available data for all six characteristics can be used in the statistical analysis, therefore this study explores only 13 species.

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Table 1—Oak species and their growth and reproductive characteristics[a]

Species	Acorns	Age	Longevity	Height	Shade	Xylem	Repro.	Growth	r&K
Quercus alba	3.11	40	300	54	3	2	1.46	0.65	1.06
Q. stellata	0.98	25	320	45	1	2	-0.30	-0.60	-0.45
Q. macrocarpa	4.98	35	340	35	4	2	2.77	2.89	2.83
Q. muehlenbergii	0.94	40	250	50	2	2	-0.20	0.07	-0.06
Q. rubra	2.98	25	130	55	3	1	-0.19	-0.41	-0.30
Q. velutina	1.52	20	175	62	3	1	-0.45	-0.53	-0.49
Q. coccinea	1.58	20	120	62	1	1	-0.54	-1.15	-0.84
Q. falcate	0.67	25	150	57	2	1	-0.62	-0.78	-0.70
Q. palustris	0.91	26	130	70	2	1	-0.59	-0.91	-0.75
Q. marilandica	0.94	20	200	30	2	1	-0.55	-0.18	-0.37
Q. bicolor	3.11	20	325	60	3	2	0.44	0.45	0.44
Q. lyrata	2.67	27	350	40	3	2	0.73	1.40	1.07
Q. texana	3.93	5	120	90	2	1	-0.63	-1.03	-0.83

[a] The column headings are species = oak genus, acorn = acorns weight (g), age = age of first reproduction, longevity = estimated maximum tree age in years, height (growth rate) = median site index (feet) at 50 years (the reciprocal was used in index calculations), shade = shade tolerance rating, xylem = wood conductance type, repro. = normalized reproductive variable index, growth = normalized growth variable index, and r&K = r and K index value. Acorn weight (1 pound per number of acorns) and the reciprocal of height were used in calculating indices.

Growth and Reproductive Characteristics

Data on oak growth and reproductive characteristics come from a number of sources. Reproductive data on acorn weight, age of reproduction and tree longevity were found in Schopmeyer (1974), Foster and Ashe (1908), Miller and Lamb (1985), Nixon (1997). Burns and Honkala (1990), Brown and Panshin 1940, Panshin and ed Zeeuw (1970) were sources of data for the growth-related physiological attributes of shade tolerance and potential conductivity as well as longevity, age of first reproduction. Height growth (in feet) derived from median site index curves for oak species were used to estimate the rate of height growth (Carmean and others 1989).

Acorn weight is an important reproductive characteristic because large acorn size confers a reproductive and competitive advantage to oaks in highly competitive environments such as forests and prairies. Long and Jones (1996) found that among 14 oak species larger acorns consistently produced larger seedlings. Large acorns probably represent a K-strategy attribute as light, wind dispersed seeds - common with trees of prodigious seed output- suggests an r-strategy. We used the weight of an acorn in fractions of a pound in all analyses.

Organisms that reproduce early in their life have an advantage in capturing resources in environments with high rates of disturbance that may provide many opportunities for reproduction. Early reproductive age is a r-strategy attribute (Pianka 1999).

Longevity of individual trees confers a variety of selective advantages, including reproduction, in that the trees will have opportunities to reproduce over a longer period. Competitive advantages of longevity are numerous also, e.g. long term site occupation and exploitation of resources. Long-lived species are generally considered K-strategists.

Rapid growth confers an advantage to species in capturing resources in non-competitive environments with high rates of disturbance, thus representing a r-selective attribute. We used both height growth and potential stem nutrient transport as measures of growth potential. We used the reciprocal of height growth at 50 years in calculating the index to match positive trends in shade tolerance and longitudinal permeability among oak species.

The longitudinal permeability of tree stems effects stem water transport and can limit the supply of water and nutrients to the crown (Kozlowski and others 1991) and thus growth. Xylem permeability is conceptualized as a trade off between safety and conductance (Lambers and others 1998). Increased conductance may maximize growth but increases the risk of cavitations and negative physiological effects. The cost of risky anatomical structure of the red oak group corresponds to the r-strategy of many species that maximize growth in response to competitive selection pressures. The red and white oaks have many xylem characteristics that differentiate the potential conductance (and thus maximum growth) of these species groups such as vessel element size, as tyloses formation in vessels, and distinct heartwood-sapwood boundaries. For example, red oak heartwood is about 100,000 times more permeable than white oak heartwood (Siau 1971). Red oak vessel elements are larger than those of white oak (Brown and Panshin 1940). We used a value of 1 for the white group and a value of 2 for the red oak group to reflect differences in potential growth due to xylem conductance.

Shade tolerance can confer a competitive advantage to young oak trees under varying degrees of competition for light. Shade tolerance classes (Burns and Honkala 1990) were quantified as 1 for very intolerant, 2 for intolerant, 3 for intermediate, 4 for tolerant, and 5 for very tolerant. Tolerance for growth under shady conditions is a K strategy attribute.

R and K Index

We created an r and K index for oak species to examine differences among oak species and to test this concept with the spatial distribution of oak species and temporal change in oak species abundance. The r and K indices were constructed for reproductive and growth related factors presented above and based on plant selection theory (Grime 1979). Three reproductive characteristics were multiplied: (1) age of first acorn production (in years), (2) species longevity (in years), (3) and acorn weight (acorns per lb.). These values were then normalized (mean of 0 and a standard deviation of 1) to create a reproductive index. Three growth characteristics were multiplied: (1) height growth at 50 years, (2) shade tolerance class, (3) and heartwood permeability class. These values were then normalized (mean of 0 and a standard deviation of 1) to create a growth index. The mean of the reproductive and growth indices is the r and K index.

Data for the abundance, distribution, and dominance of oak species is derived from studies resulting from the Missouri Ozark Forest Ecosystem Project (MOFEP) (Brookshire and Shifley 1997, Kabrick and others 1997). This project is an experiment to assess the landscape level impacts of management practices on forest ecosystems including wildlife, plants, and forest productivity.

Data describing disturbance frequency, fire frequency, and the development and values of disturbance indices are taken from Guyette and Kabrick (2002). Fire frequency was estimated with regressions developed from fire scar chronologies at 26 sites in the Current River watershed (Guyette and others 2002, Guyette and Dey 2000). Mean fire interval estimates in this study are for the period of maximum variation in fire frequency among sites, the years 1700 to 1850. Only five of the 13 oak species (white, post, black, scarlet and red oak) grow at the MOFEP study sites, thus only five oak species could be used in testing predictions made by the r and K index approach about how species oak may be related to disturbance at these sites.

RESULTS

Oak reproductive and growth characteristics were significantly correlated using two methods. Pearson correlation analysis of reproductive and growth indices showed significance ($r = 0.94$, $p < 0.001$) among oak species attributes (fig. 1). Multivariate analysis using among growth and reproductive resulted in a canonical correlation coefficient of 0.98 ($p < 0.01$). All individual growth and reproductive variables were positively correlated but only acorn weight versus shade tolerance ($r = 0.54$, $p = 0.03$) and longevity versus permeability ($r = 0.94$, $p < 0.01$) were strongly correlated. Correlation analyses indicate that the distribution of all measured characteristics among species is consistent with the theoretical predictions of r and K life history strategies.

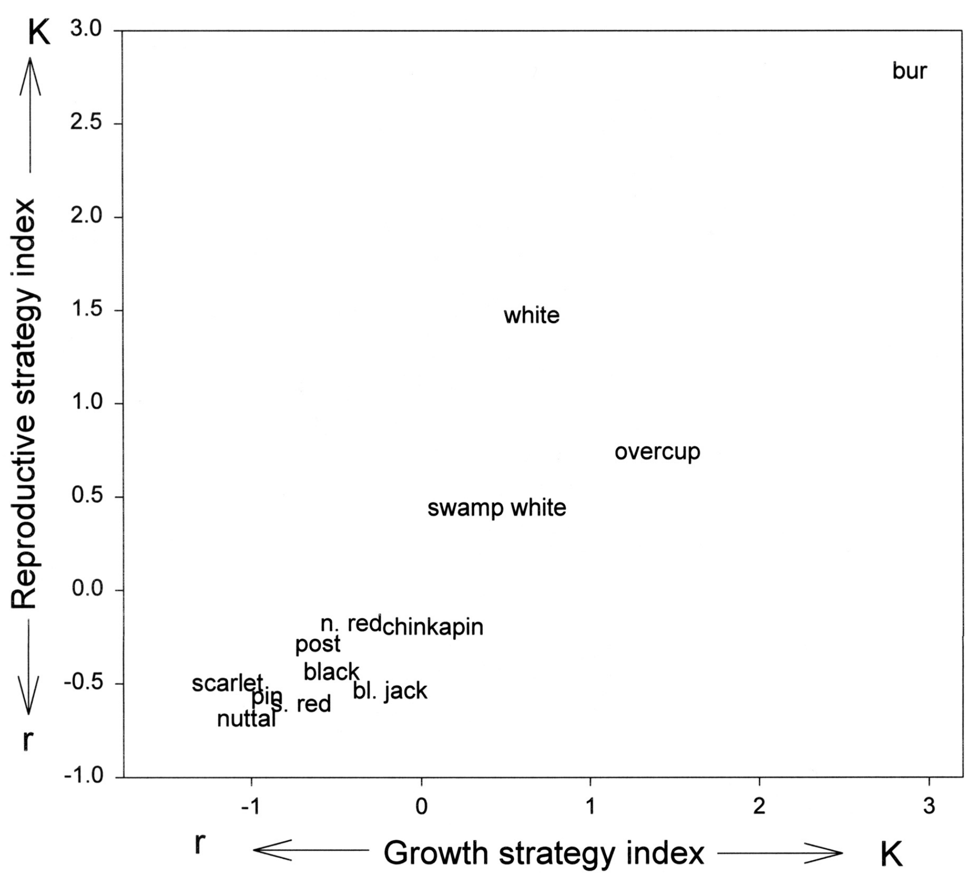

Figure 1—Scatter plot of the relationship between indices of the reproductive and growth strategies of 13 oak species (see table 1 for details).

The distribution of oak species at the nine large (> 314 ha) sites (Missouri Ozark Forest Ecosystem Project) was related to their r and K index values and the long-term disturbance histories of the sites (fig. 2). The abundance of five oak species that grow at these sites was weighted by their r and K index value and was correlated (r = 0.71, p = 0.03) with index values of long-term disturbance frequency (Guyette and Kabrick 2002).

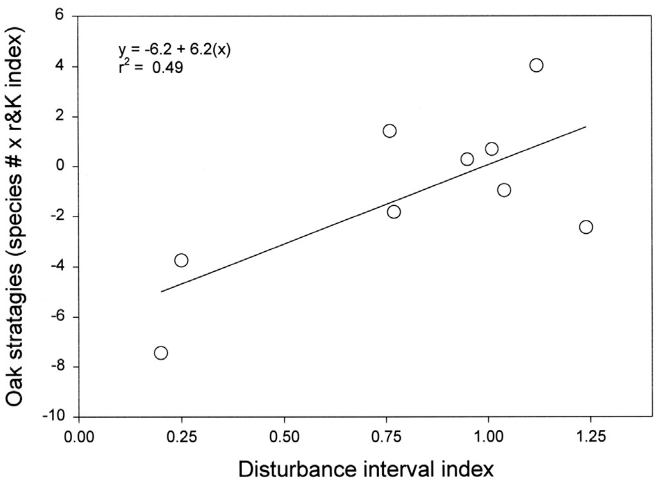

Figure 2—Scatter plot illustrating the relationship between the abundance of oak strategies (number oak by species x r and K index, summed by site) and disturbance history at the nine MOFEP sites.

Recent changes in the abundances of oak species at the nine MOFEP sites are consistent with their life history strategies and their r and K index values. Ten years of inventory data (1992-2002) measured in undisturbed, permanent vegetation plots show that the net basal area of oaks with high r and K indices such as white oak are increasing while those species with low r and K indices such as black jack are decreasing (fig. 3). These abundance changes at these undisturbed sites are roughly correlated with their r and K index values.

DISCUSSION

Non-random associations among growth and reproductive characteristics of oak indicate a distribution of attributes that is consistent with r and K selection processes that has occurred over an evolutionary time scale in response to disturbance and competition. The development of an r and K index among the species of a genus may have utility in management as well as scientific research. Quantification of species strategies could aid in predicting forest composition in response to silvicultural prescriptions. Residual basal area left after logging may be used in the prediction of species regeneration. Scientist might use the r and K index values to explain species distributions. For example,

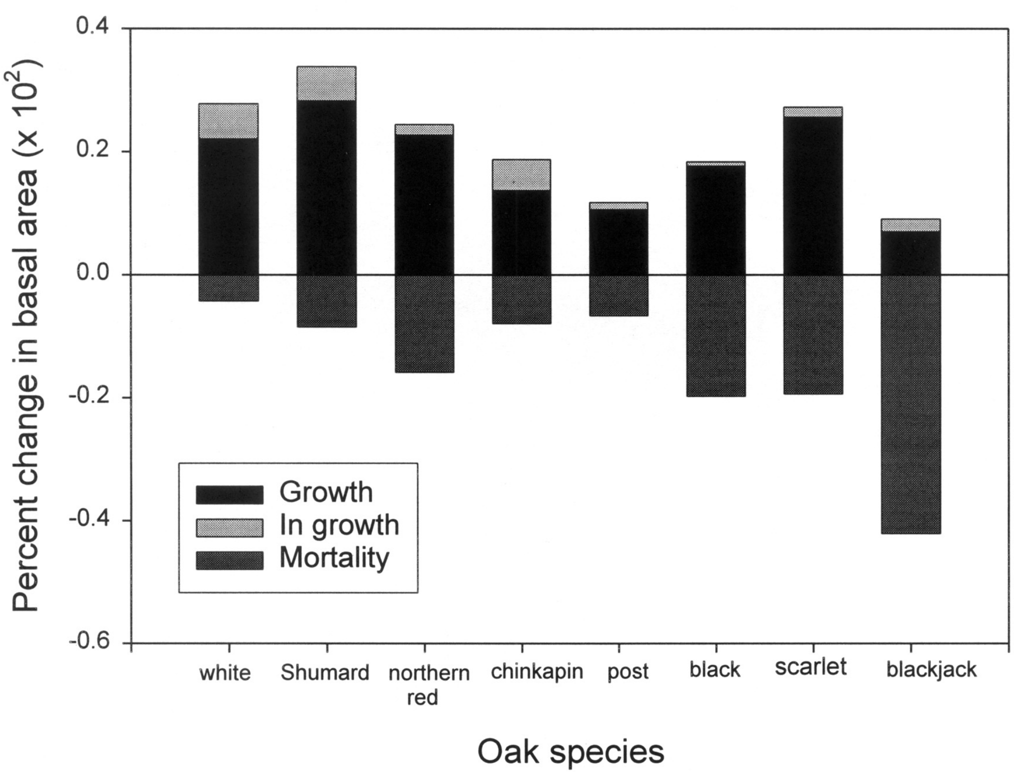

Figure 3—Growth, in-growth, and mortality for oaks at the nine MOFEP sites in undisturbed plots during 1992-2002. Growth is average basal area increases for trees >4.5 in. in diameter at breast height (d.b.h.); in-growth is average basal area increases by trees originally <4.5 in. in d.b.h. that grew into the larger size class during the sampling period; mortality is basal area of trees that died during the sampling period.

bur oak, an extreme K strategist (table 1), only occurs in many areas in extremely competitive environments such as flood plain forests and in tall grass prairies where large seeds and a high degree of shade tolerance allow for initial regeneration.

CONCLUSIONS

Quantitative comparisons among the life history strategies of oak and other large genera via index values are possible, may prove of value, but have limitations. We used values found in the oak literature. There is considerable difficulty in finding precise quantitative data that are comparable among a number of species. For instance, although we found excellent data on acorn weight, other variables such as the age of first reproduction or shade tolerance were more qualitative – more expert opinion than actual measured quantities. Thus, we believe that it should be understood, that when using the numeric values of r and K indices, these values only qualitatively estimate differences among species life history traits.

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LITERATURE CITED

Brookshire, B.L.; Shifley, S.R. 1997. Proceedings of the Missouri Ozark Forest Ecosystem Project symposium: An experimental approach to landscape research, 1997 June 3-5, St. Louis, MO. Gen. Tech. Rep. NC-193. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 378 p.

Brown, H.P.; Panshin, A.J. 1940. Commercial timbers of the United States. McGraw-Hill Book Comp. New York. 554 p.

Burns, R.M.; Honkala, B.H. 1990. Silvics of North America. Vol. 2, Hardwoods. Agriculture Handbook 654. USDA Forest Service. Washington DC. 877 p.

Carmean, W.H.; Hahn, J.T.; Jacobs, R.D. 1989. Site index curves for forest tree species in the Eastern United States. North Central Forest Exp. Station. GTR NC-128. 142 p.

Crawley, M.J. 1997. Plant ecology. Blackwell Science. London. 715 p.

Flora of North America Editorial Committee. 1997. Flora of North America. Vol. 3. Oxford Univ. Press. New York. 590 p.

Foster, H.D.; Ashe, W.W. 1908. Chestnut oak in the Southern Appalachians. USDA Forest Service. Circular 135. Government Printing Office. Washington DC. p 21.

Gleason, H.A.; Cronquist, A. 1991 Manual of vascular plants of Northeastern United States and adjacent Canada. The New York Botanical Garden, Brox New York. 910 p.

Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley & Sons. New York. 222 p.

Guyette, R.P.; Dey, D.C. 2000. Humans, topography, and wildland fire: the ingredients for long-term patterns in ecosystems. In: Proceeding: Workshop on fire, people, and the Central Hardwood Landscape, D.A. Yaussey, compiler. GTR NE-274, 129 p.

Guyette, R.P.; Kabrick, J.M. 2002. The legacy and continuity of forest disturbance, succession, and species at the MOFEP sites. In: Proceedings of the second Missouri Ozark Forest Ecosystem Project symposium (Shifley and Kabrick eds.). USDA Forest Service. GTR NC-227. 227 p.

Guyette, R.P.; Muzika, R.M.; Dey, D.C. 2002. Dynamics of an anthropogenic fire regime. Ecosystems 5: 472-486.

Kabrick, J.M.; Larsen, D.R.; Shifley, S.R.1997. Analysis of pre-treatment woody vegetation and environmental data for the Missouri Ozark Forest Ecosystem Project. In: Brookshire, B.L.; Shifley, S.R. eds. Proceedings of the Missouri Ozark Forest Ecosystem Project symposium: An experimental approach to landscape research. Gen. Tech. Rep. NC-193. St. Paul, MN: U.S. 378 p.

Kozlowski, T.T.; Kramer, J.P.; Pallardy, S.G. 1991. The physiological ecology of woody plants. Academic Press, Inc. NY. 657 p.

Lambers, H.; Chapin, F.S., III; Pons, T.L. 1998. Plant physiological ecology. Springer, New York. 540 p.

Long, T.J.; Jones, R.H. 1996. Seedling growth strategies and seed size effects in fourteen oak species native to different soil moisture habitats. Trees 11: 1-8.

MacArthur, R.H.; Wilson, E.O. 1967. The theory of island biogeography. Princeton Univ. Press. Princeton, New Jersey.

Miller, H.A.; Lamb, S.H. 1985. Oaks of North America. Naturegraph Publishers, Inc. Happy Camp. California. 327 p.

Nixon, K.C. 1997. *Qurecus*. In: Morin, N.R. eds. Flora of North America Vol 3. Oxford Univ. Press. New York. 590 p.

Odum, E.P. 1997. Ecology a bridge between science and society. Sinauer Associates, Inc. Sunderland, Massachusetts. 330 p.

Panshin, A.J.; de Zeeuw, C. 1970. Textbook of wood technology. McGraw-Hill Book Comp. New York. 705 p.

Pianka, E.R. 1999. *Evolutionary ecology*. Sixth Edition. Benjamin-Cummings.

Schopmeyer, C.S. 1974. Seeds of woody plants in the United States. USDA Forest Sevice, Dep. Agric. Handbook No. 450. Washington, D.C.

Siau, J.F. 1971. Flow in wood. Syracuse Univ. Press. Syracuse. New York. 131 p.