

REGRESSION ANALYSIS OF SAPLING ABUNDANCE
IN THE INNER BLUEGRASS OF KENTUCKY WITH
SPECIAL REFERENCE TO SEED SOURCE

Julian J.N. Campbell
School of Biological Sciences

D. B. Richards
Department of Forestry

and

Lillie R.F. Crowley
Department of Mathematics
University of Kentucky
Lexington, Kentucky 40506

ABSTRACT

Multiple regression analysis is applied to density and basal area of sapling species in the Inner Bluegrass of Kentucky, primarily to estimate the local effect of parent trees on sapling abundance. Small-seeded wind or bird-dispersed species have moderate positive relationships with parent trees, while large-seeded nut or legume producers have strongly positive or slightly negative slopes. These differences are interpreted in terms of seed weight, dispersal and attraction of granivores. Other relationships are with cattle grazing, herbaceous cover, total basal area, fertility, slope, aspect and topographic position.

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INTRODUCTION

This study was primarily designed to estimate by regression analysis the dependence of sapling abundance on parent tree abundance in the same area as part of a model of forest succession. Data on forest succession from which basic processes may be studied, is scanty. Instead it has been common practice to predict succession from sapling distribution in relation to canopy (e.g. Braun, 1950). However, this approach has not been developed very far until recently (Horn, 1975; Fox, 1977). Both kinds of data have led to transition matrix models of succession in which each canopy type is given a set of probabilities that it will change into the various possible replacing types in a certain time. The species composition of the saplings beneath a particular canopy species has been claimed to estimate these probabilities. Little attention has been given to testing the assumption of constancy in sapling composition and to finding out what local factors, other than the canopy type directly above, are influencing sapling species. Horn (1975) has suggested making transition probabilities dependent on current canopy abundance of replacing species to express the spatial dependence of reproduction on seed source from parent trees. The regression analysis undertaken here is a first step towards estimating such seed source effects for different species.

Data used in this study are from the Inner Bluegrass of central Kentucky, a plateau of Ordovician limestone. This area was largely free of closed forest at the time of settlement in the 1770's (Braun, 1950; Davidson, 1950), presumably due to some combination of Indian effects, fire, grazing and periodic drought. Upland fields still contain isolated old oaks (Quercus macrocarpa, Q. muhlenbergii) and ashes (Fraxinus quadrangulata), relics of presettlement savannah. Colonization by closed forest of fallow fields is spontaneous today. Most old-growth forest, with Acer saccharum and some Fagus grandifolia as potential dominants on mesic sites, is in gorges along the Kentucky River where the above-mentioned factors and agriculture have had less effect. Species restricted to gorges were omitted from the regression analysis.

METHODS

All data used in the analysis come from 114 circular plots, mostly with diameter 30 m, that were surveyed in the summer of 1977. A third of the plots were centered on dead trees and their areas match those of the canopy openings, generally 15-30 m in diameter. Trees, that is individuals over 10 cm d.b.h. (diameter at breast height), and saplings, individuals from 1-10 cm d.b.h., were measured for d.b.h. Saplings were recorded only from an inner concentric plot of 20 m diameter, except in the dead tree-centered plots. The plots were selected systematically with respect to the central species of tree in order to provide some minimum variety for comparative studies. They are all from the following Counties of Kentucky: Fayette, Franklin, Jessamine, Scott and Woodford.

Dependent variables in the regression equations are:

- N = Numbers per hectare of saplings belonging to a particular species.
 B = Basal area (m^2/ha) of saplings belonging to a particular species.

Independent variables used are:

- T = Topographic position from ridge (= 10) to flooded bottom (= 60)
 S = Slope of ground in percent (= $100 \times$ tangent of angle)
 F = Fertility of soil based on U.S. Soil Conservation Service soil surveys (1-5 scale) - (U.S.D.A. 1968, 1977 and unpublished)
 G = Grazing intensity by cattle based on visual signs such as cattle, cattle paths, state of herbaceous vegetation, faeces and accessibility (0-3 scale)
 H = Herbaceous cover in percent
 A = Total tree basal area of all species (m^2/ha)
 P = Parent (conspecific) tree basal area (m^2/ha)

The following variables were used to express the combined influence of slope and aspect (Stage, 1976):

- Ss = Slope x sine of aspect measured clockwise from magnetic North
 Ss2 = Slope x sine of twice the aspect angle
 Sc = Slope x cosine of aspect angle
 Sc2 = Slope x cosine of twice the aspect angle.

The following quadratic terms were used:

- T^2 , to allow for mid-slope species,
 P^2 , to allow for saturation by seed source of safe sites or self-inhibition.

An interaction term (F x G) was added after initial runs since several species showed relationships to both F (fertility) and G (grazing).

In the step-wise procedure used (Statistical Analysis System) independent variables were added in turn that maximized the variation in dependent variable accounted for by the regression equation (R^2 = multiple correlation coefficient). Some measurements of independent variables, especially "grazing", "fertility" and parent basal area as seed source, are no doubt subject to considerable error. If error were correlated with magnitude of variable, the significance testing of this (Model 1) analysis would be partially invalidated (Sokal and Rohlf, 1969), but there is no reason to expect such correlation. In any case this analysis was undertaken as much in the spirit of hypothesis generation as in that of hypothesis testing. The final equations selected are significant at the 5% level, but contain all slopes significant at the 10% level.

RESULTS

The following are the species of saplings, the regression equations and the variation accounted for (R^2):

Acer saccharum Marsh. (sugar maple) combined with Acer nigrum Michx. f. (black maple) $(R^2 = 34\%)$

$N = 276 - 4.86 T + 15.3 S$
 $B = 0.632 - 0.0234 T + 0.000269 T^2 + 0.0197 S - 0.00829 A + 0.0319 P$ $(R^2 = 49\%)$

Aesculus glabra Willd. (Ohio buckeye)

$N = 23.5 + 223 P - 26.1 P^2$ $(R^2 = 32\%)$
 $B = -0.0301 - 0.00239 Sc + 0.444 P - 0.0522 P^2$ $(R^2 = 40\%)$

Carya cordiformis (Wang) K. Koch. (bitternut hickory)

$N = -36.6 - 0.00748 T^2 + 5.13 FG + 2.07 A + 6.31 P$ $(R^2 = 23\%)$
 $B = 0.0153 - 0.000782 Sc^2 + 0.00513 FG + 0.00427 P^2$ $(R^2 = 31\%)$

Carya laciniosa (Michx. f.) Loud. (kingnut hickory)

$N = 1.58 - 3.12 FG + 14.8 G + 42.2 P - 10.8 P^2$ $(R^2 = 24\%)$
 $B = 0.00364 - 0.00726 FG + 0.0328 G + 0.0759 P$ $(R^2 = 36\%)$

Celtis occidentalis L. (hackberry)

$N = -178 + 12.9 T - 0.225 T^2 - 4.42 S + 9.76 A + 2.29 P^2$ $(R^2 = 25\%)$
 $B = 0.279 - 0.00616 S - 0.0912 G + 0.0756 P - 0.00296 P^2$ $(R^2 = 11\%)$

Fagus grandifolia Ehrh. (beech)

$N = 0.819 - 0.0623 S + 15.4 P - 1.78 P^2$ $(R^2 = 59\%)$
 $B = 0.00143 - 0.000120 S + 0.0408 P - 0.00565 P^2$ $(R^2 = 56\%)$

Fraxinus americana L. (white ash)

$N = 81.5 - 1.84 Sc^2 - 21.3 G$ $(R^2 = 9\%)$
 $B = 0.216 - 0.00908 T + 0.000156 T^2 - 0.00488 Sc - 0.122 G + 0.0240 FG$
 $+ 0.0196 P - 0.000505 P^2$ $(R^2 = 15\%)$

Fraxinus quadrangulata Michx. (blue ash)

$N = 76.6 - 2.51 T + 1.39 H + 50.8 P - 5.72 P^2$ $(R^2 = 15\%)$
 $B = 0.0180 + 0.180 P - 0.0186 P^2$ $(R^2 = 11\%)$

Gleditsia triacanthos L. (honey locust)

$N = 17.8 - 3.51 F + 1.61 FG - 6.88 G$ $(R^2 = 9\%)$
 $B = 0.0440 - 0.00900 F + 0.00375 FG - 0.0163 G$ $(R^2 = 12\%)$

Gymnocladus dioica (L.) K. Koch. (Kentucky coffeetree)

$N = -0.0325 + 2.00 G + 7.33 P$ $(R^2 = 42\%)$
 $B = -0.000463 + 0.00589 G + 0.0280 P$ $(R^2 = 49\%)$

Juglans nigra L. (black walnut)

$N = 9.21 - 0.00219 T^2 - 1.75 F + 0.103 H$ $(R^2 = 13\%)$
 $B = 0.0249 - 0.000406 T - 0.000363 S$ $(R^2 = 6\%)$

Liriodendron tulipifera L. (yellow poplar)

(for N regression is not significant)
 $B = 0.00388 - 0.000127 Sc + 0.000291 Sc^2$ $(R^2 = 4\%)$

Prunus serotina Ehrh. (black cherry)

$$N = -46.3 - 1.34 S + 19.1 F + 9.14 P$$

$$(R^2 = 12\%)$$

$$B = -0.0826 - 0.0250 S + 0.0344 F + 0.0205 P.$$

$$(R^2 = 12\%)$$

Quercus macrocarpa Michx. (burr oak)

$$N = 7.14 - 0.129 S + 0.555 FG$$

$$(R^2 = 6\%)$$

$$B = 0.0110 - 0.00000641 T^2 + 0.00255 FG$$

$$(R^2 = 5\%)$$

Quercus muhlenbergii Gray (chinquapin oak)

$$N = 12.9 + 1.50 S - 0.906 Sc - 0.221 P^2$$

$$(R^2 = 18\%)$$

$$B = 0.0691 - 0.0000195 T^2 + 0.00221 S - 0.00205 Sc - 0.000492 P^2$$

$$(R^2 = 25\%)$$

Quercus shumardii Buckl. (Shumard oak)

$$N = 5.30 - 0.244 Sc$$

$$(R^2 = 3\%)$$

(for B regression is not significant)

Robinia pseudoacacia L. (black locust)

$$N = 5.25 - 0.977 F - 1.05 G + 1.46 P$$

$$(R^2 = 24\%)$$

$$B = 0.00113 - 0.000149 T + 0.000190 H$$

$$(R^2 = 7\%)$$

Tilia americana L. (basswood)

(+ T. heterophylla Vent. on a few plots)

$$N = -69.0 + 4.15 T - 0.0505 T^2 + 1.08 S + 0.857 Sc^2 + 9.65 P$$

$$(R^2 = 23\%)$$

$$B = 0.00163 + 0.000798 S + 0.00107 Sc^2 - 0.000674 Sc + 0.00962 P$$

$$(R^2 = 13\%)$$

Ulmus americana L. (White elm)

$$N = 1313 + 0.259 T^2 - 318 F + 166 FG - 835 G$$

$$(R^2 = 25\%)$$

$$B = 1.12 - 0.00560 S - 0.217 F + 0.0904 FG - 0.655 G - 0.00557 H \\ + 0.0908 P$$

$$(R^2 = 29\%)$$

Ulmus rubra Muhl. (slippery elm)

$$N = 192 - 4.55 Ss - 3.86 Sc^2 - 3.19 H$$

$$(R^2 = 11\%)$$

$$B = 0.166 - 0.00413 Sc - 0.00311 H$$

$$(R^2 = 8\%)$$

For comparison of species' parent tree relationships, the regression slopes are expressed (figure 1) as percentages of the regression estimates at average site conditions for each species, but without parent trees on the plot ($P = 0$). This is done to take account of density independent factors that determine the general abundance of a sapling species, namely seed numbers produced per parent tree and the various environmental constraints on the species. For species with quadratic terms the regression estimates at parent tree basal areas of $1 \text{ m}^2/\text{ha}$ (instead of the linear term) are expressed as similar percentages. This allows comparison at a low basal area of parent species. Also shown in figure 1 are the parent basal areas at the peaks in sapling curves, for rough comparison at greater parent basal areas. Non-significant slopes are included as best estimates since it is likely that some real slopes are masked by the great residual variation.

Table 1 summarizes other significant relationships arranged by independent variable.

Table 1. Non-seed source relationships arranged by independent variable.

Total Basal Area (A):

negative: *Acer saccharum*

positive: *Carya cordiformis*
Celtis occidentalis

Herbaceous cover (H):

negative: *Ulmus americana*
Ulmus rubra

positive: *Fraxinus quadrangulata*
Juglans nigra
Robinia pseudoacacia

Grazing (G):

negative: *Celtis occidentalis*
Fraxinus americana
Gleditsia triacanthos
Robinia pseudoacacia
Ulmus americana

positive: *Carya laciniosa*
Gymnocladus dioica

Grazing x Fertility (FG):

negative: *Carya laciniosa*

positive: *Carya cordiformis*
Fraxinus americana
Gleditsia triacanthos
Quercus macrocarpa
Ulmus americana

Fertility (F):

negative: *Gleditsia triacanthos*
Juglans nigra
Robinia pseudoacacia
Ulmus americana

positive: *Prunus serotina*

Aspect:

southerly: *Liriodendron tulipifera*
Quercus muhlenbergii
Quercus shumardii
Tilia americana
Ulmus americana

east-west: *Carya cordiformis*
Fraxinus americana

Topographic position (T):

negative: *Acer saccharum* (N)
Carya cordiformis
Fraxinus quadrangulata
Juglans nigra
Quercus macrocarpa
Quercus muhlenbergii
Robinia pseudoacacia

positive: *Ulmus americana*
minimum at T = 43: *Acer saccharum*
maximum at T = 42: *Tilia americana*
maximum at T = 29: *Celtis occidentalis*
minimum at T = 28: *Fraxinus americana*

Slope (S):

negative: *Celtis occidentalis*
Fagus grandifolia
Juglans nigra
Prunus serotina
Quercus macrocarpa
Ulmus americana

positive: *Acer saccharum*
Quercus muhlenbergii
Tilia americana

DISCUSSION

The amount of variation explained by these equations (R^2) is at most 59%, with half of them accounting for less than 15%. But this is comparable with another attempt to regress tree abundance (Martin and DeSelm, 1976) even though more detailed site data was used in that study. The great residual variation here is probably due to error in measurement of some independent variables, especially grazing, fertility and seed source. Also, most variables are only indirect measures of the environment impinging on the plant. Finally, historical random disturbance will have masked more stable relationships.

Parent tree relationships

Interpretation of positive conspecific tree relationships solely in terms of seed source effects is questionable. They may also be due to conspecific trees acting as indicators of suitable sites for growth and survival of that species, especially since the site variables used are themselves indirect indicators of the immediate plant environment. But, as far as we know, species that have steeper slopes do not generally have greater site sensitivity.

Small-seeded wind or bird-dispersed species have moderate positive slopes (figure 1), whereas large-seeded nut or legume producing trees have either strongly positive slopes, or, in the case of all 3 Quercus species and Juglans, small negative slopes. The only significant slopes that do not fit this pattern are of Carya cordiformis (N and B) and Fraxinus quadrangulata (B). C. cordiformis has the second smallest nut here. Of the eleven non-significant slopes only two, one each of Liriodendron and Quercus macrocarpa, do not fit.

The production of numerous small seeds and their dispersal over great distances by wind or birds may restrict the size of the regression slopes in such species. But large seeds are attractive to granivores and these animals may concentrate their feeding near seed producing trees. Thus large-seeded species may develop negative slopes unless granivory is resisted.

The presence of unusual toxins in seeds has been shown for Aesculus, Gymnocladus and Robinia (Fowells, 1965; Janzen, 1976; Rosenthal, 1977), and these species all have high slopes. It may be significant that Fagus and Aesculus, which have the highest slopes (at 1 m²/ha), are the only two species to have prickly fruit. Avoidance of granivores by temporary satiation has been suggested for Fagaceae (Janzen, 1971) but available seed crop interval data (Schopmeyer 1974) show no relationship with regression slope size.

While there is no overall relationship between slope and general competitive tolerance (e.g. Fowells, 1965; Baker, 1949), differences in tolerance, perhaps enhanced by intraspecific competition and other specific pests, may be involved in comparisons of slope between related species (e.g. Fagus is more tolerant than Quercus, Carya more so than Juglans). Robinia is well known to proliferate by root sprouts (Fowells, 1965) which may explain its high slope. Fagus, the only other species here with a reputation for lateral spread by root sprouts, especially in northern forests (Braun, 1950), has a high slope, but we have not observed convincing root sprouting in the Inner Bluegrass.

Strong negative quadratic terms in the parent tree relationship are found mostly in the heavy seeded species (figure 1). These could be due to increase in concentration of granivores, dispersers or other factors involved in self-inhibition as parent basal area increases. Despite the toxicity of Aesculus and Robinia, which exhibit self-inhibition, squirrels will use buckeyes in small quantity (Fowells, 1965) and both species can suffer from defoliators (Fowells, 1965). Gymnocladus, which does not show self-inhibition, is remarkably free of pests (Janzen, 1976). Negative quadratic terms are also found for Celtis (B), Fraxinus americana and F. quadrangulata, but the tree basal area at the peak is much higher (13 and 20 m²/ha) in the former two species than in the nut trees (0-4 m²/ha). In Carya cordiformis and Celtis (N) positive quadratic terms are found. Small seed size, and bitter taste in Carya cordiformis, may enable these species to resist granivores.

Other biotic relationships (table 1)

Total basal area: Only three significant terms were found (Acer saccharum (B) - negative, Carya cordiformis (N) and Celtis (N) - both positive). This probably indicates the inadequacy of basal area as a measure of competitive influence. The effect of canopy species and age may be very important (Fox, 1977; J. Campbell, unpublished). C. cordiformis and Celtis may accumulate as small saplings under old trees, but Acer saccharum, while often accumulating in deep shade, is very responsive to canopy openings (Bray, 1956; J. Campbell, unpublished).

Herbaceous cover: Both Ulmus species have negative terms, while Juglans, Robinia and Fraxinus quadrangulata have positive terms. The Ulmus species have the smallest seeds here, while Juglans has the second largest. Presumably seed reserves are of value for establishment in dense ground vegetation. Also, Juglans and Robinia are known to be allelopathic against herbaceous vegetation (Rice, 1974). Allelopathy may enable a species to be more abundant in dense ground vegetation than in other areas where adverse factors such as tree competition may act. None of the species with positive herbaceous terms become dominant as saplings in these plots, hence a significant suppression of total herbaceous growth, counteracting their association with herbaceous cover, is unlikely. Herbaceous growth is greatest under light canopies, so these positive slopes may simply be an expression of intolerance. Juglans and Robinia are intolerant, but F. quadrangulata is moderately tolerant (unpublished) and other species here are also intolerant.

Grazing: Carya laciniosa, Gymnocladus, Quercus macrocarpa and Carya cordiformis have positive cattle grazing terms, the latter two as part of an interaction with fertility. Except for C. cordiformis, these species are relatively western in distribution and may be adapted to grazing pressure in grassland openings that extended as far east as the Bluegrass. Q. macrocarpa and the other species in smaller numbers are part of old savannah vegetation. Ulmus americana, Gleditsia and Robinia have negative grazing and fertility terms but positive interaction terms (the latter is non-significant for Robinia). These three species are thicket-forming invaders of grazed pasture, and, except for Ulmus americana, they are also western in distribution. The interaction in these species may be due to a subtle balance involving the responses of growth and palatability to fertility, and local increase in fertility due to defaecation. The palatability of Ulmus spp to deer and cattle is related to N content and soil fertility (Dalrymple and Dwyer, 1965; George and Powell, 1977). Celtis and Fraxinus americana, which have negative terms, are common invaders of the grassland pioneers. Generally these relationships are in accord with the limited data on palatability

and toxicity of tree species (e.g. Fowells, 1965; Muenscher, 1966; Pogge, 1967; Herron and LaBone, 1972; Dwyer, 1961). F. americana, Celtis, Gleditsia and less consistently Ulmus and Robinia are reported palatable. Robinia and Gleditsia have thorns, and Robinia, Gymnocladus and Quercus spp can be lethally toxic. The absence of grazing responses for late successional species may be due to their restriction to steeper slopes where there is too little grazing for comparison of plots.

Abiotic Relationships (table 1)

These are generally in accord with known moisture preferences. The abundance of several species on southerly slopes may reflect increased insolation. Since flatter topography is more disturbed, species more abundant there are generally interpreted as less tolerant of tree competition, better dispersed, and more tolerant of grassland competition. But pH decreases and soil depth increases with decreasing slope (U.S.D.A., 1968), and presumably microclimate changes, so these factors should also be candidates for consideration. The positive relationship of Fagus to flat topography reflects occurrence on terraces and concave slopes in gorges, not on the upland plateau. Fertility is less than "high" or "moderately high" only on ridges and in swamps, hence the scarcity of its involvement in regression equations independently of topographic position and grazing.

Fraxinus quadrangulata

This species is rarely discussed in the literature. Here it is odd in being a small seeded species with strong linear and negative quadratic relationships to parent trees, and with a positive relationship to herbaceous cover. Other grassland invaders, especially other western species, have commonly been shown to be allelopathic (Rice, 1974). Van Shipp (of the Buckley Hills Audubon Society, Woodford County) has shown one of us (J.C.) evidence of inhibitory effect by open grown F. quadrangulata on his tobacco that was too clear cut to be shade-induced. These circumstantial pieces of evidence suggest an allelopathic influence on itself and herbaceous vegetation.

SUMMARY

- Interpretation of the regression analysis is as follows: (a) Rather than merely acting as indicators of favorable sites, local conspecific tree basal area relationships reflect seed source effects.
- (b) Small-seeded wind or bird-dispersed species have moderate positive parent tree relationships, but large-seeded nut or legume producing species have strongly positive or negative relationships. Large seeds are not dispersed away from parent trees if granivores are resisted with toxins, prickles etc., but otherwise such species may be subject to depletion of seed concentrated on parent trees. This may also explain the negative quadratic terms of several large-seeded species.
- (c) Other factors involved in some parent tree relationships may be root sprouting, competitive tolerance, allelopathy and other specific pests.
- (d) Few sapling species are related to total basal area, suggesting basal area is too broad an index of competition, combining different canopy species and sizes.
- (e) Abundance in dense herbaceous vegetation is related to seed size and allelopathy.
- (f) Cattle grazing resistance is related to western distribution, position in

grassland succession, toxicity and palatability. There may be a complex interaction involving response of growth and palatability to fertility, and cattle mineral cycling.

(g) Many species are related to topographic position, slope and aspect in accord with moisture preference and competitive tolerance since southerly aspects and gentler slopes are more open to saplings of some species.

(h) Circumstantial evidence suggests that Fraxinus quadrangulata may be allelopathic.

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