RECENT CHANGES IN THE POPULATION STRUCTURE OF BLACK WALNUT

Walter F. Beineke [1]

Black walnut *(Juglans nigra* L.) over the years has been the most highly prized and sought-after American wood. Due to this popularity, high-quality black walnut, which never held a position of great abundance in the deciduous forest, has been cut into near oblivion in some parts of its range. Cutting has removed many of the best phenotypes, thus drastically reducing the gene pool.

While this is serious enough, a more insidious phenomenon may be taking place. Clearing of the forest in the Midwest, beginning 100 years ago, left rather small isolated blocks of trees. Within these small blocks, there are often a few walnut trees remaining. If pollen flight and seed dispersal distances are relatively short, these few black walnut trees make up the breeding population of that area. Therefore, selfing and, hence, inbreeding depression may be adding to the poor quality of the next generation of naturally reproduced black walnut.

INBREEDING VS. OUTCROSSING

Black walnut is monoecious, bears anemophilous unisexual flowers, and is normally an out-crossed species; although, from controlled pollination experiments and field observation it is apparent that black walnut is easily self-pollinated. Research in progress by the author shows that self-pollination of black walnut produces seed set equal to or greater than outcrossing (Table 1). In addition, Wood (1934) made thousands of self-pollinations in many cultivars of Persian walnut *(Juglans regia* L.) and found that, "each variety was... markedly self-fertile."

Table 1. Percent of control-pollinated and open-pollinated black walnut flowers producing normal seed

Selection number	Control-pollinated		Open-pollinated
	Selfed	Outcrossed	
		Percent	
102	35	29	0
118	23	20	41
34	19	14	61
Weighted mean	22	18	49

Dichogamy usually insures that flowers are not self-pollinated in black walnut. Unfortunately, weather conditions often interfere with this theoretically sound arrangement, and pollen is found ripening at the time of female flower receptivity on the same tree. Inbred seedlings are the result. Most inbred seedlings lack vigor and are unable to compete in the forest environment.

Black walnut is intolerant and does require light. In deciduous forest openings, vigorous competition usually develops among many tree, shrub, and herbaceous species. Seedlings that are the product of selfing or related matings would be eliminated, and, thus, no new walnut seedlings would become established in the next generation of the forest. This could account for the paucity of naturally occurring black walnut seedlings in forest openings with seed sources nearby. On the other hand, if inbred seedlings occasionally did survive to maturity, it would contribute to further degradation of the following generation of forest trees.

Selfed seed gathered for pampered nursery-grown seedlings may be the reason that many walnut plantations perform so poorly. Seedlings are culled by most nurseries, but seedlings sold are often small and grow much slower than larger seedlings (Williams, 1965).

In preliminary work by the author, seedlings that are the product of control-pollinated selling have shown depressed growth, compared to control-pollinated outcrossed and open-pollinated seedlings from the same trees (Table 2). Results from three female parent trees are combined in Table 2. The percent germination of the selfed seed was lower than either the outcrossed or open-pollinated seed, but it could be adequate to allow for the establishment of inbred seedlings in the forest situation (Table 2).

Table 2. Percent germination and first-year height of control-pollinated and open-pollinated black walnut seedlings

	Control – pollinated		Open-pollinated
	Selfed	Outcrossed	
Number of seedlings	32	35	47
Percent germination	72.7	81.4	97.9
Mean seedling height (feet)	1.55	1.66	1.72
Percent height increase over the self		7.1	11.0

Observations by the author indicate that self pollination does occur under natural conditions. We have collected nuts and grown seedlings from one black walnut tree for five consecutive years. In two of the five years, seedlings produced by this tree have been ranked first or third in height in half-sib progeny tests. In the other three years, they have been among the shortest in our progeny tests. In addition, seed set and germination

[1] Associate Professor of Forestry, Department of Forestry & Conservation, Purdue University, West Lafayette, Indiana 47907.

have been low in those three years. The female flowers become receptive at the same time that antithesis occurs on this tree. Therefore, it is assumed that the three years of depressed seedling growth, seed set, and germination from this tree are the result of inbreeding.

Inbreeding depression has been confirmed in a wide variety of other woody plant families. For example, in the Pinaceae, all genera show growth depression and reduced vigor of inbred seedlings (Franklin, 1970). Inbreeding depression has also been found in species related to black walnut. In pecan (*Carya illinoensis* [Wangenh.] K. Koch), inbred seedlings were 23 percent shorter than cross-pollinated seedlings produced by the same tree (Romberg and Smith, 1946). Serr and Forde (1956) found 3 of 45 selfed Payne cultivar Persian walnut seedlings were dwarfed, low in vigor, and susceptible to winter die-back. In general, the selfs had fewer desirable qualities and lower vigor than Payne crossed with other cultivars.

Assuming that outcrossing occurs more frequently than inbreeding in black walnut, what is the fate of the outcrossed individual in these small isolated woodlands? The few poor-quality individuals left for breeding purposes probably perpetuate their kind; but, in addition, lacking pollination from sources outside the small, isolated woodland, the progenies will tend to become homozygous at additional loci in future generations, and undesirable genes could become fixed due to genetic drift (Wright, 1931).

POLLEN DISPERSION

Black walnut is wind-pollinated; thus, the possibility exists that pollen could be carried by air currents from individuals located considerable distances from a small woodlot. Several factors mitigate against such occurrences, including pollen morphology and pollen viability. Black walnut has no inflated bladder-like extensions as does most coniferous pollen, so it is unable to sail as easily as "winged" pollen. Several researchers have found wind-dispersed pollen many miles from its source (Anderson, 1963; Illy and Sopena, 1963; Sarvas, 1955; Silen, 1962). Pollen, however, must contact a receptive female stigma to have any chance of effective survival. To this author's knowledge, no studies have been attempted to find the viability of pollen after traveling long distances. In all probability the viability would be extremely low, which would further mitigate against chance long-distance pollination, particularly in black walnut.

The larger the pollen grain, the heavier and less likely it is to be carried long distances by air currents. Black walnut pollen is larger than the anemophilous pollen of many other species. For instance, black walnut pollen averages approximately 34 p in diameter compared to giant ragweed (*Ambrosia trifida* L.) 17 **p,** American sycamore (*Platanus occidentalis* L.) 20 **p,** ash (*Fraxinus* spp.) 24 p, poplar (*Populus* spp.) 25 **p,** birch (*Betula* spp.) 20-30p, and white oak (*Quercus alba* L.) 26 x 34 ,u (Wodehouse, 1935). Some species having larger pollen than black walnut include: sweetgum (*Liquidambar styraciflua* L.) 35 **p,** and American elm (*Ulmus amencana* L.) 30 x 37 ,u (Wodehouse, 1935). Most coniferous pollen is larger than black walnut (Cain, 1940). However, the pines (*Pinus* spp.), spruces (*Picea* spp.), and firs (*Abies* spp.) have large, inflated, bladder-like wings which act as sails.

Thus, black walnut pollen probably doesn't travel as far as the pollen of some other anemophilous species. Tests with Persian walnut pollen, which is somewhat larger than black walnut pollen, have shown that Persian walnut pollen may be carried up to one mile from its source, but its effective distance is only 200 to 300 feet (Griggs, 1953). Wood (1934) calculated that a stigma of Persian walnut in the lower branches of a tree would receive approximately 192 pollen grains while a stigma 500 feet from the pollen source under ideal conditions would receive only 24 grains, and a stigma at one-half mile would receive no pollen.

Tests indicate that black walnut pollen remains viable at room temperature less than 48 hours (unpublished research in progress by author). A sharp loss of viability occurs 12-24 hours after anthesis. It appears highly unlikely that pollen from more than a short distance could be a factor in pollinating trees in small woodlots.

Koski (1970) contends that pollen of all anemophilous species can be carried long distances in a "pollen cloud" regardless of pollen size and that background pollen (i.e., pollen from outside the stand) depends more on the density of the species in the area. For example, Norway spruce (*Picea abies [L.] Karst.*) accounted for 35 percent of the trees in the area and the proportion of background pollen was 63 percent. However, a low-density species such as alder (*Alnus* spp.) accounting for only 4 percent of the trees, had only 15 percent background pollen. Black walnut is a low-density species in most areas of the Eastern Unitied States.

If black walnut pollen is carried long distances in a "pollen cloud," two criteria of its effectiveness must be met. First, pollen must encounter a receptive stigma upon its fallout, and, second, the pollen grain must be viable. Both events occurring simultaneously in black walnut seem most unlikely.

Pollen viability is relatively low in walnut. The average viability of fresh Persian walnut pollen is approximately 23 percent (Wood, 1934). Fresh black walnut pollen averages somewhat higher. Our studies indicate 40 to 60 percent pollen viability in black walnut. Many pollen grains that fail to germinate appear to be devoid of protoplasm, and, therefore, are lighter in weight. These dead pollen grains would tend to carry farther from their point of origin than viable grains.

Wright (1952) found actual pollen dispersal distances for several tree species (not including black walnut) to be much less than theoretically proposed by Schmidt (1918), and Dyakowska (1936). Sluder (1969) states that Wright's breeding unit sizes, "were so small that, if they are realistic, large variation in gene frequency occurs over short distances in species with scattered distribution or distribution along narrow stream bottoms. Even in well-distributed species there occur many gaps large enough to hinder gene flow."

It could be argued that if the pollen of walnut has an effective distance of only 200-300 feet, then walnut has been breeding in small populations over eons of time. However, during the glacial periods walnut migrated before the advancing ice sheets or followed the retreating edge north (Polunin, 1960). Depending on the site, walnut probably occurred every few hundred feet in most deciduous forests of the Central States as it does today in uncut woodlots. Therefore, it is probable that a mixing of genes could readily occur among trees within stands and among nearby stands until relatively recent times when cutting destroyed the pattern of continuous forest.

The seed is another method of transportation for black walnut gene packages. However, except on rare occasion when nuts are washed into streams and transported, nuts stored by squirrels and other mammals are usually carried less than 300 feet from the tree of origin (Clark, 1970).

SUMMARY

By relying on natural regeneration in black walnut, from scattered high-graded remnants in wood lots, small, isolated breeding populations are developing. Self-pollination is effective and inbreeding depression does occur in black walnut. Due to genetic drift and matings between closely related individuals, increasingly homozygous, low vigor, slow growing, disease prone, and poorly formed black walnut trees probably are being produced. When black walnut pollen size, shape, mobility, viability, and abundance is considered, it becomes evident that walnut pollen is probably not effective over long distances, thus, reinforcing these small inbred populations.

This paper is not intended to be a dogmatic statement of truth, and much research must be accomplshed to ascertain additional facts. However, it is intended to stimulate thought so that we can begin to understand the true impact of man on the once continuous forest in the Central States.

One way to reverse the trend of dysgenic selection and inbreeding depression is to establish clonal seed orchards from the best remaining individuals and to carefully insure their crossbreeding in the orchard, and to plant the resultant seedlings not only in plantations, but in forest openings as well. Thus, the argument for establishing seed orchards for black walnut is intensified, and the urgency already evident in this endeavor takes on added meaning when the breeding habits and population dynamics of this species are considered.

LITERATURE CITED

Andersson, E. 1963. Seed stands and seed orchards in the breeding of conifers. World Consult. on Forest Genetics and Forest Tree Imp. Proc. II. FAO/FORGEN 63-8/1:1-18.

Cain, S. A. 1940. The identification of species in fossil pollen of *Pinus* by size-frequency determination. Amer. J. Bot. *27:* 301-308.

Clark, F. B. 1970. Measures necessary for natural regeneration of oaks, yellow-poplar, sweetgum, and black walnut. p. 1-16. *In* the silviculture of oaks and associated species. U.S.D.A. Forest Service Paper NE-144.

Dyakowska, J. 1936. Researches on the rapidity of the falling down of pollen of some trees. Polska Akademja Umiejetnosci Kracow Wydzial Matematyczno-przyrodniczy Bull. Internat. Ser. B. Sci. Nat. 1:155-168.

Franklin, E. C. 1970. Survey of mutant forms and inbreeding depression in species of the family Pinaceae. U.S.D.A. Forest Service Research Paper SE-61.

Griggs, W. H. 1953. Pollination requirements of fruits and nuts. Calif. Agr. Exp. Sta. Serv. Cir. 424, 35 p.

Illy, G.,and Sopena, J. 1963. La dispersion du pollen de pin maritime. Rev. for franc. 15: 7-18.

Koski, V. 1970. A study of pollen dispersal as a mechanism of gene flow in conifers. Metsantutkimuslaitoksen Julkaisuja 70.4, Helsinki, Finland, 78 p.

Polunin, N. 1960. Introduction to plant geography. McGraw-Hill Book Co., Inc., New York, N.Y. 640 p.

Romberg, L. D.,and C. L. Smith. 1946. Effects of cross pollination, self pollination, and sib-pollination on the dropping, the volume, and the kernel development of pecan nuts and the vigor of seedlings. Proc. Amer. Soc. Hort. Sci. 47: 130-138.

Sarvas, R. 1955. Ein Beitrag zur Fernverbreitung des Blu· enstaubes einiger Waldbume. Z. Forstgenet. v. Forstpflanzenz. 4:137-142.

Schmidt, W. 1918. Die Verbreitung von Samen and Blatenstaub Burch die Luftbewegung. Osterr. Bot. Ztschr. 57:313-328.

Serr, E. F.,and Forde, H. I. 1956. Walnut breeding. Proc. Amer. Soc. Hort. Sci. 68: 184-194.

Silen, R. R. 1962. Pollen dispersal considerations for Douglas-fir. J. Forestry 60: 790-795.

Sluder, E. R. 1969. Gene flow patterns in forest tree species and implications for tree breeding. Second World Consultation on Forest Tree Breeding FO-FTB-69-9/7 : 1-9.

Williams, R. D. 1965. Plant large black walnut seedlings for best survival and growth. U.S.D.A. Forest Service Paper CS-38, 5 p.

Wodehouse, R. P. 1935. Pollen grains. McGraw-Hill Book Co., Inc., New York, N.Y. 574 p.

Wood, M. N. 1934. Pollination and blooming habits of the Persian walnut in California. U.S.D.A. Tech. Bull. 387, 56 p.

Wright, J. W. 1952. Pollen dispersion of some forest trees. U.S.D.A. Forest Service. Northeastern Forest Exp. Sta. Pap. 46, 42 p.

Wright, S. 1931. Evolution in Mendelian populations. Genetics 16: 97-159.