

The Evolutionary Role of Wildfire in the Northern Rockies and Implications for Resource Managers

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PURPOSE

FIRE is a natural part of Northern Rocky Mountain terrestrial ecosystems. These, like any ecosystems, operate, in part, through interactions of living organisms. The biological interrelationships have developed from the processes of organic evolution, which result from the functioning of genetic mechanisms. For reasons made clear later, fuel and fire specialists, to understand their potential influence on evolutionary processes, daily should be asking themselves questions about genetic principles.

My purpose here is to raise questions. They are questions I hope fuel and fire specialists will be asking themselves as they proceed through their day-to-day decision-making in fuel and fire management. As they ask themselves the questions, these specialists may wish to better equip themselves with the tools of modern genetic principles.

My second purpose is to try to stimulate research. Only the generation of good data will confirm or refute the concerns raised here.

GENETIC PRINCIPLES

Consider first, genetic variability. One source of genetic variability is the sexual process. Meiosis assort and recombines genes in the first meiotic division. The sexual process also recombines genes when gametes unite in fertilization.

Genetic variability is generated by the normal sexual process—meiosis and union of gametes—independent of the four primary forces of evolution. These are natural selection, mutation, migration, and random genetic drift.

Let us examine each of these four forces, one at a time. Natural selection is the “differential and nonrandom reproduction of different genotypes . . .” (Rieger, et al., 1968). Individuals best able to reproduce in a particular environment contribute their genes, in their offspring, in highest proportions in the next generation. Selection working gradually over many generations, then, results in a population better adapted to that environment.

The second force, migration, is the “systematic movement of genes between populations . . .” (Ford-Robertson, 1971). Pollen may travel hundreds of miles from its tree of origin (Erdtman, 1954) in its migration. Seed, too, can be an effective vehicle for carrying genes far from their source (further discussed later). However, distance between populations is usually an effective barrier to migration. Wright (1962, p. 26) concludes that, “Small, equal-sized populations separated by two or three miles may be considered as isolated.” Standing trees also may serve as a partial barrier to pollen migration (Snyder, 1972).

The third evolutionary force mutation, occurs in two forms. The first is chromosomal aberration. Here, chromosomes have become abnormally arranged. There may be extra pieces of chromosomes floating in the nucleus, or a chromosome may be missing a segment, or perhaps there are too many or too few whole chromosomes. An example of a chromosome mutation in humans is mongolism, caused by an extra chromosome (Burns, 1972).

The second form of mutation is gene mutation. Genes are sequences of “rungs” (called bases) in the ladder-like DNA molecule. DNA in the chromosome is the blueprint for all life processes and structures of the organism. Gene mutations are “unprogrammed” changes in

the “rungs.” Among environmental factors which induce mutations is heat (Dobzhansky, 1970). Others are certain irradiations and chemicals.

The final primary evolutionary force is random genetic drift. It may operate as an important changer of gene frequencies in populations of Northern Rocky Mountain forest trees. Random genetic drift is change in gene frequencies due to chance alone. The changes result from random mating of very small breeding populations. I illustrate by modifying an hypothetical example authored by Ehrlich and Holm (1963). Let us assume that we have a barrel of 20,000 marbles—10,000 white and 10,000 black. The marbles represent gametes, any two of which can unite. The colors represent different alleles—different forms of the gene—10,000 black alleles and 10,000 white ones. We draw a random sample of 2,000 from this barrel of 20,000 marbles. In our sample are 979 black marbles and 1,021 white ones. The frequency of the black marbles has changed from .5000 to .4895. The deviation from a 50-50 ratio in the sample is likely to be relatively minor when the initial population and sample size are large.

Assume now a barrel of 1,000 marbles, 500 black and 500 white, and draw 10 at random. In our sample we draw, by chance, six black and four white. Here, the frequency of the black marbles has changed from .5000 to .6000, nearly a tenfold larger change than in the preceding example. This illustrates that, by chance, fluctuations around the mean—around the expected 50-50 ratio—are likely to be large when we are sampling from a small population and our sample size is small. We can conclude that, by chance alone, we may get substantial deviations from the allelic ratio of the original population, if we start with a small breeding population.

FIRE'S EVOLUTIONARY ROLE

What role may fire have played as a possible mutagen or agent of migration, selection or genetic drift? Consider the roles individually.

FIRE MAY FUNCTION AS A MUTAGEN

Fire generates heat, and as cited earlier, heat is a known mutagen. It is possible that heat could induce mutations in trees surviving low-

intensity fires. However, I know of no direct evidence of this in forest trees.

FIRE MAY FUNCTION AS AN AGENT OF MIGRATION

Fire may remove trees standing as a barrier to pollen flight between distant populations, and in doing so, alter the pattern of pollen migration. By removing vegetation fire may also serve as a builder of "runways" for the transport of seed over snow surfaces in winter. This phenomenon, called "scudding," is often observed, especially in openings, by Northern Rocky Mountain foresters (On, 1975), and is reported as a seed dispersal mechanism for lodgepole pine (Crossley, 1955) and western larch (Shearer, 1975).

FIRE MAY FUNCTION AS A SELECTION AGENT

These six adaptive traits, and many others not listed, probably result from the natural selection force of fire on Northern Rocky Mountain conifers:

1. Insulative bark (most notable in old trees of western larch, Douglas-fir, ponderosa pine).
2. Seed transportability, especially in western larch and Douglas-fir.
3. Allelopathy: fire influences the capacity of one plant community to produce products inhibiting the development of another plant community (Harrington, 1974).
4. Development and maintenance of flammability, as suggested by Mutch (1970).
5. Cone serotiny in lodgepole pine (Lotan, 1967; Lotan, 1968; Perry and Lotan, manuscript).
6. Possible suppression of the development of genetic resistance in tree species to some indigenous pests (Howe, 1973). Fire periodically removes the selection pressure of the pest so that insufficient generations of hosts are exposed to build genetic resistance. Roth (1953, 1966) suggests this interaction for ponderosa pine and dwarf mistletoe. Heinselman (1971) suggests that 20th Century forest fire suppression has made some insect (e.g., spruce budworm) and disease outbreaks more prevalent, implicating the dominant role of fire (vs. tree genes?) in controlling some pests.

FIRE MAY FUNCTION AS AN AGENT OF RANDOM GENETIC DRIFT

Major wildfires in the Northern Rockies leave islands of live trees partially or wholly isolated from external pollen sources. I conclude that trees in these small, presumably random mating, populations serve as the parents for most of the ensuing natural regeneration (except for serotinous-cone species). These may be ideal situations for major changes in gene frequencies by chance alone. If so, we would expect to find many currently non-adaptive traits in Northern Rocky Mountain tree species, i.e., more and different genetic variation than would be created by the normal sexual process in large breeding populations. For example, I am unable to envision any current adaptive value to purple versus normal green or brown cone color in western white pine (Steinhoff, 1974). Perhaps the color difference will have adaptive value in some future environment.

EVOLUTIONARY CONSEQUENCES OF ALTERNATIVE MANAGEMENT REGIMES

Consider, now, two fire and fuel management alternatives based on contrasting sets of assumptions. Contrast the probable evolutionary consequences resulting from each.

ALTERNATIVE 1

Assume first that wildfire exclusion becomes a reality and that none of wildfire's forms is simulated by prescribed burning. Neither of these assumptions is likely to become reality, but they are chosen because they simplify our modeling of possible evolutionary consequences.

Consequences on mutation. If indeed the heat of fire has served as a mutagen, the exclusion of fire would reduce the frequency of mutations. These are the raw material of evolution, the new genes among which selection chooses. Mutation rate reductions caused by fire exclusion would probably be minor in the total population of mutations from all causes, and thus insignificant in future evolution.

Consequences on migration. Isolation barriers or partial barriers (intervening vegetation) gradually will become more frequent, reducing gene exchange over long distances. We would expect some losses in

traits broadly adaptive over large geographic areas. Falconer (1960) demonstrates mathematically that total genetic variance over a botanical range could be expected to increase with increases in isolation barriers. Both loss of adaptation and increase in variance probably would be minor.

Consequences on selection. Here, we must differentiate between weakly heritable and strongly heritable traits. The former are usually controlled by many genes (polygenic inheritance), the latter by one (simple inheritance) or a very few (oligogenic inheritance) genes. At a given, moderately high selection intensity and intermediate gene frequency, the occurrence of a weakly heritable trait changes almost imperceptibly in one or a few generations, while that of a simply inherited trait changes spectacularly.

Most fire-adaptive traits would be lost only very slowly, as most are probably polygenic and weakly heritable. Lodgepole pine cone serotiny (and that of other closed-cone pines) appears to be an exception. This trait may be controlled by as few as two or three genes (Perry and Lotan, manuscript; Rudolph, et al., 1959). Predominant serotiny could change to predominant non-serotiny in two to three tree generations with fire exclusion. (A generation in lodgepole pine may be as short as 4 years in wild stands.)

If we consider fire to have been the dominant control of some insects and diseases, we could speculate that fire's exclusion would permit the pests' selection pressures to begin working on host populations. Thus, the process of building genetic resistance in the hosts might start. It would likely be a very slow and unpredictable process; some host populations might become extinct as a result. Forest protection might face a major insect and disease control problem. I suggest that fire's role here may be of sufficient importance to argue strongly against any policy approaching that of fire exclusion.

Consequences on random genetic drift. If random genetic drift results from the interbreeding of trees in very small islands surviving major wildfires, then exclusion of fire will eliminate this source of genetic drift. Drift may be an important creator of genetic variability in all Northern Rocky Mountain conifers except lodgepole pine. Isolated fire survivors are the most common—though not the only—genetic bottleneck found in the Northern Rockies. As such, fire sur-

vivors may be the region's most important source of random genetic drift, and the phenomenon of sufficient significance to argue against a policy of fire exclusion.

ALTERNATIVE 2

The second [assumption] alternative is more realistic as a future fire and fuel management regime. Here, we assume, contrary to Beaufait (1971, 1974), that major conflagrations will be prevented. (Beaufait (1974) doubts that wildfires of 30,000 to 50,000 acres can be prevented even when all commercial forest lands are intensively managed.) At the same time, prescribed fire will be used in areas averaging 40 to 60 acres, and up to 300 acres, but infrequently in understories (only under old Douglas-fir, western larch or ponderosa pine).

This regime would approximate most forms of natural wildfire. Effects of prescribed fire as an agent of selection and of migration would likely be the same as those of natural wildfire. With reduced understory burning, however, might come a reduced induction of mutations (but insignificant), assuming wildfire's heat to be a mutagen in forest trees.

The principal evolutionary consequence of this fire and fuel management regime would be in altering fire's probable role as an agent of random genetic drift. Prevention of major conflagrations (or simulation of their effects) would eliminate the ingredients for drift, i.e., the replacement of large, continuous populations by tiny islands of isolated interbreeders from which most ensuing regeneration would emanate. Clearings of 300 acres could not provide the breeding isolation essential to set the stage for genetic drift. Again, a potentially important creator of genetic variability could be lost.

SUMMARY

Fire and fuel management in the Northern Rockies could have major evolutionary consequences, particularly in fire's role as an agent of random genetic drift. Research must either allay these fears or show resource managers how to simulate fire's beneficial effects in a world becoming, by necessity, increasingly intolerant of wildfire. In the meantime, the resource manager must equip himself with the

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tools of modern evolutionary understanding—just as he is doing with ecological principles—to avoid dysgenic fire and fuel management policies and practices.

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