MODULE 4
Forest Management

Case study 4.2

Does selective logging degrade the genetic quality of succeeding generations through dysgenic selection?

Jonathan Cornelius

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Introduction

The purpose of forest tree breeding is to progressively improve the genetic quality of planting stock. This has often been achieved through ensuring that each successive generation is produced from only the genetically best trees of the preceding one. Essentially, dysgenic selection is the opposite of this process and causes a negative change in genetic quality over one or more generations. It has been suggested that it could occur as a consequence of selective logging: if loggers remove the 'best' trees, then only poorer trees remain to produce the next generation. The concept is logical and simple; however, as we shall see, the conditions under which dysgenic selection could occur are not as widespread as this might suggest.

This exercise allows you to explore the theme of dysgenic selection by considering a particular logging operation in big-leaf mahogany (*Swietenia macrophylla* G. King). You will form groups of three to five people, each of which will be assigned one or more of three tasks:

- Task 1. Discuss whether, in this logging operation, dysgenic selection would be likely to occur
- Task 2. Formulate a general set of risk factors that would suggest susceptibility to dysgenic selection
- Task 3. Discuss the consequences of dysgenic selection and how it can be mitigated

Each task is explained more fully at the end of the case study.

At the end of the exercise you should be able to:

- identify situations in which dysgenic selection is likely to occur (or not occur) and
- explain to forest managers, certifying agencies and others why a given silvicultural regime might or might not lead to dysgenic selection.

To attempt the exercise, you will need to understand how to quantify and predict the impact of dysgenic selection. You will also need some background information on the ecological characteristics of mahogany. These areas are covered below.

Exploring dysgenic selection: response to selection and the 'breeders' equation'

"There is nothing more practical than a good theory" (Kurt Lewin)

There are no clearly documented cases of dysgenic selection that has been caused by logging, but this may be because it has never been properly investigated scientifically (e.g. by comparing the growth of seedlings from harvested and remnant trees). Therefore, dysgenic selection remains somewhat hypothetical. However, the genetic theory of artificial selection is well developed; relevant parts are outlined below, initially with illustrations from tree improvement, as, in a sense, dysgenic selection is tree improvement in reverse.

The response to selection

In tree improvement, the following general approach is commonly used:

- In populations currently used as seed sources, the phenotypically best trees are selected
- Seed is collected from these trees
- This seed is used to establish a new seed-production population (after which the cycle can begin again).

The aim of this process is to improve, generation by generation, the genetic quality of the population, i.e. the population mean for one or more commercially important traits. The change in the population mean from generation to generation is known as the **response to selection**.

The response to selection can be measured using field trials in which the progeny of selected and unselected trees are compared (Box 1). In such experiments, we know that the response to selection is due to a genetic change in the population because the two sets of progeny were grown under the same environmental conditions in the same field experiment.

In the case of dysgenic selection resulting from logging, the response to selection would be negative rather than positive, because the trees that will provide the seed for the next generation will be those left by loggers. Thus, a negative response might have occurred in the example in Box 1 if "SSO [seedling seed orchard] routine" progeny had been compared with seed collected from the 20 worst trees per ha rather than comparing them with seed from the best trees.

Box 1. Realized response to selection in *Acacia auriculiformis*

A field trial of *Acacia auriculiformis* A. Cunn. in Vietnam included, among other treatments, 'SSO routine' (progeny grown from seed from average-quality trees in a seedling seed orchard [SSO]) and 'SSO select' (progeny grown from seed from the phenotypically best 20 trees per ha in the seed orchard, ranked on an index combining both growth rate and form).

In the field trial, mean height at 4 years of the SSO select progeny (representing the subsequent, improved generation) was 9.72 m, compared with 9.15 m for the SSO routine progeny (representing the previous generation). In this case, therefore, response to selection (R) from one generation to the next was:

$$R = 9.72 \text{ m} - 9.15 \text{ m} = 0.57 \text{ m}$$

or an improvement equivalent to 6.2% of the SSO routine mean of 9.15 m.

Source: Hai PH, Harwood C, Kha LD, Pinyopusarerk K, Thinh HH. 2008. Genetic gain from breeding Acacia auriculiformis in Vietnam. *Journal of Tropical Forest Science* 20(4): 313–327.

Predicting response: the breeders' equation

The response to selection calculated in Box 1 is known as the realized response, as it is a response that has already occurred. Unfortunately, there are no published studies of realized response in the case of dysgenic selection. However, genetic theory provides us with tools to predict the response to selection. This is done using the 'breeders' equation', the simplest form of which is:

Predicted response to selection (R) = selection differential (S) x heritability (h^2)

Selection differential

The selection differential [S] (Box 2) is a within-generation measure of the phenotypic superiority of the selected trees, i.e. the parents of the next, improved generation. In the example in Box 2, production of this new generation would require either controlled pollinations between the selected trees or their establishment (as grafts) in a clonal seed orchard isolated from external pollen sources, where they could cross-pollinate with each other. Alternatively, open-pollinated seed could be collected from phenotypically superior trees ('plus-trees'), but in this case the pollen parents would be unselected trees and the selection differential would be halved.

Note also that the selection differential assumes that every tree contributes the same number of offspring to the next generation. When this is not the case, the individual phenotypic values would need to be weighted by the contribution of each individual to the next generation.

Box 2. Selection differential in *Pinus caribaea* var. *hondurensis* (Sénéclauze) W.H.Barrett & Golfari in Puerto Rico

Thirty-six phenotypically superior 'plus-trees' were selected in 16-year-old *Pinus caribaea* var. *hondurensis* plantations in Puerto Rico. The mean individual tree volume of 36 selected trees was 0.848 m^3, compared with the mean individual tree volume in the population of 0.324 m^3. The selection differential for individual tree volume was therefore:

$$S = 0.848\ m^3 - 0.324\ m^3 = 0.524\ m^3$$

Source: Ledig FT, Whitmore JL. 1981. *The calculation of selection differential and selection intensity to predict gain in a tree improvement program for plantation-grown Honduras pine in Puerto Rico*. Research Paper SO-170. USDA Forest Service, Southern Forest Experiment Station, New Orleans, LA, USA.

Heritability

Commercial traits of timber trees, such as growth rate or stem form, tend to be polygenic traits. This means that many genes influence them, rather than just one or two. In addition, environmental effects, such as soil type, affect them. Both factors cause phenotypic variation between individuals. Heritability (h^2) expresses the degree to which inherited genetic factors, rather than environmental and other non-heritable factors, influence the phenotypic variation for a given trait. Heritability varies from zero (no heritable genetic effect on phenotypic variation) to one (all the phenotypic variation is heritable).

Heritability also expresses the degree to which the within-generation selection differential, which is a phenotypic differential, is expected to lead to a between-generation, inherited, response to selection.

Heritability values are specific to particular populations, traits and locations, because their values depend on allele frequencies and on environmental variation. However, some broad generalizations can be made. In many cases, phenotypic variation is mostly non-heritable. Estimates of heritability for growth and form traits in forest trees typically fall in the range 0.1–0.3; specific gravity is notable in that it usually has a higher value (>0.3). Other traits in both timber and other trees may have much higher values. For example, heritabilities of ≥0.55 have been reported for heartwood proportion in teak, height:width ratio in pear fruits and yield in rubber.

Estimation of heritability generally requires establishment of progeny tests made up of treatments with known degrees of genetic relationship (e.g. half-siblings). In natural forests, there is no easy way of estimating heritabilities. However, Namkoong's[1] view that heritability values for growth traits within the highly variable environments of natural forest are likely to be around 0.05 seems reasonable—particularly as, in natural forest, age differences can also cause phenotypic variation. Traits with higher heritabilities are likely to be less affected by highly variable natural forest conditions as, by definition, their phenotypic variation tends to be less influenced by the environment.

Using the breeders' equation

In the *Pinus caribaea* example referred to in Box 2, the researchers used an estimated heritability for individual tree volume of 0.11. With this, they were able to predict a response to selection of:

$$R = Sh^2 = [0.524\ \text{m}^3]0.11 = 0.058\ \text{m}^3$$

This is equivalent to 18% greater individual tree volume at 16 years, given the unimproved mean individual tree volume of 0.324m^3.

The breeders' equation applied to dysgenic selection

Here, we apply the breeders' equation to dysgenic selection using a hypothetical example.

Species X is a fast-growing tree species valued for its timber. The large, monospecific, even-aged stands are logged when about 6 years old, when the mean dbh of a typical tree might be about 30 cm. Loggers leave only the smallest trees of species X—about one in every 100—with a mean dbh of 15 cm. The species shows high genetic variation in growth rate, but environmental factors such as soil, competition, predators, etc. also have strong effects on growth rate. As a result, the differences in growth rate between trees (i.e. the phenotypic variation) are mostly environmental in origin ($h^2 = 0.3$). Logging is carried out before the flowers are pollinated, and seedlings are unable to survive under a mature canopy. As a consequence, only trees left by loggers contribute to the next generation. There are always large geographical distances between populations, such that different populations are reproductively isolated. After six years, previously harvested areas can be logged again.

In this case, the predicted response to selection is:

$$R = Sh^2\ [15\ \text{cm} - 30\ \text{cm}]0.3 = -4.5\ \text{cm}$$

In strict terms, this means that if we were to measure the dbh of all the trees in the next generation (or a sample of them) at the same age at which logging took place (6 years), we would expect the mean to be 30 – 4.5 = 25.5 cm, a 15% decline in dbh. Less strictly, we could interpret this to mean that growth rate is predicted to decrease by 15%.

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[1] Namkoong G. 1970. Optimum allocation of selection intensity in two stages of truncation selection. *Biometrics* 26: 465–476.

Clearly, a 15% decline in productivity would constitute a considerable dysgenic effect. As you read and discuss the case study, you may find it useful to compare the assumptions used for species X with the real example of mahogany.

The breeders' equation predicts the impact of selection over one generation. Both theory and experimental results indicate that it remains accurate for several generations of selection, so if dysgenic selection were to be applied for a number of generations, further negative responses would be expected.

Case study species

Mahogany is the most valuable Neotropical timber[2]. It has been in high demand for hundreds of years because of its combination of desirable features: beauty, high stability, durability and workability. The mahogany trade and the unsustainable logging practices it has been based on have greatly depleted many populations of all three mahogany species: *Swietenia humilis* Zucc. in the Pacific watershed of Mexico and Central America, *S. mahagoni* (L.) Jacq. in the Caribbean and Florida (USA) and *S. macrophylla* in Mexico, Central America and the Amazon basin. In addition, several authors have suggested that selective logging of mahogany may have had dysgenic effects.

This section outlines key features of the ecology and genetics of mahogany. Many of these are directly relevant to our principal concern, i.e. its possible susceptibility to dysgenic selection. Unless otherwise stated, the term mahogany applies specifically to *S. macrophylla*.

Ecology

Swietenia macrophylla has a large natural range, occurring principally in seasonally dry lowland forests from the southern Amazon, through Central America and north to the Yucatan peninsula and Veracruz State, Mexico. Trees can reach diameters of up to 2 m and heights of 60 m in suitable conditions. In plantations or in open situations, trees often have a short unbranched bole, whereas those in natural forests usually have a longer unbranched bole. This difference probably results from differential incidence of mahogany shoot borer (*Hypsipyla grandella* Zeller) attacks, which are rare on young trees in natural forests.

Mahogany produces small, monoecious flowers during the dry season; these are reportedly pollinated by small, generalist insects. As mahogany pollinators can travel distances of several kilometres, long-distance gene flow can occur. However, in larger populations there is likely to be limited pollen flow into the population from outside. Individual trees are usually strongly outcrossing. The fruits, woody capsules with 40–60 winged seeds, mature in the dry season (10–12 months after pollination). The seeds are dispersed by wind and gravity. Most seeds fall within 80 m of the mother tree. If there is sufficient moisture, seeds will germinate even in shady understory conditions. Seeds have no long-term dormancy mechanism and therefore mahogany does not form a seed bank. In natural forest, fruit production per tree varies both from year to year and from tree to tree; smaller trees (<75–80 cm dbh) generally produce few fruits.

Two patterns of frequency and abundance of mahogany trees have been noted. In the Yucatan peninsula of Mexico, mahogany can occur in groups of up to 20 trees per ha. These seem to result from the ability of mahogany to tolerate fire or hurricanes better than other tree species. Mature mahogany trees are able to

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[2] Woods such as rosewood (*Dalbergia* spp.) and lignum-vitae (*Guaiacum sanctum* L.) may trade at much higher prices on speciality markets such as those supplying hobbyist woodworkers, but the volume of trade in such species is low

survive such catastrophic disturbance, leading to higher survival of seed trees of mahogany relative to other species. Copious seed rain can then lead to high densities of seedlings (up to 1000 per ha), only a small proportion of which need to reach adulthood to produce relatively high stocking densities.

More commonly, mahogany is found in small aggregations at an average density of 0.1–3 adult trees per ha; Amazonian forest with 1–2 mahogany trees per ha would be considered 'mahogany-rich'. Although mahogany seedlings can survive for several years in shaded understory conditions, survival through to pole and later stages requires some degree of canopy opening, e.g. through tree-fall or other local, small-scale disturbance. In this more common scenario, the low density of adult trees probably reflects the low probability of canopy opening and viable mahogany regeneration occurring at the same time and place.

The dependence of regeneration on canopy disturbance suggests that groups of trees are likely to be made up of trees of similar ages.

Genetics

Little is known about the genetics of mahogany. However, the few studies carried out to date suggest that there is little genetic differentiation between mahogany populations, particularly over relatively small (subregional) distances. This finding applies to variation in both molecular markers and phenotypic traits. However, there is evidence that populations that are closer to each other tend to be genetically more similar.

The little information that is available on within-population genetic variation in mahogany suggests that, like many tropical trees, it exhibits abundant within-population variation at molecular marker loci. With regard to quantitative traits, the few heritability estimates suggest that heritabilities in mahogany are similar to those found in other species, i.e. estimates of heritabilities of growth and form traits in forest trees typically fall in the range 0.1–0.3.

Case study site and management regimes

The forest

The Marajoara forest covers an area of 4100 ha in Pará State, southeastern Brazilian Amazon. It is owned by the forest industry. It is surrounded by a matrix of pasture, smallholder agriculture and heavily logged forests. Before logging began in the 1990s, Marajoara had an average of 65 mahogany trees (>20cm) per 100 ha, considered to be high-density stocking; about 60% of these trees were >60 cm dbh. The number of trees per dbh class is shown in Figure 1. Mean dbh before logging was 67.0 cm.

Between 1997 and 2004, mean annual capsule production of trees in the 30–60 cm and >60 cm dbh classes was estimated at 3.9 and 14.5 per tree, respectively; only 1.6% of trees in the 30–60 cm range and 17.5% in the >60 cm class averaged more than 25 capsules per year. Most seeds are shed by July, relatively early in the June–October dry season. Studies of seed dispersal, germination and seedling survival suggest that, in the case of trees producing 25 capsules, around 135 seedlings (5.8 per capsule) would be expected to survive through to the end of the dry season following establishment (i.e. to approximately 15 months old).

One study monitored the fate of 1925 understorey seedlings located within 30 m of eight parent trees. After 8 years, 11 seedlings (1.3%) had survived. By contrast, among seedlings in artificially opened canopy gaps that were cleared annually up to 46 months, 43.8% of survived to 80 months old.

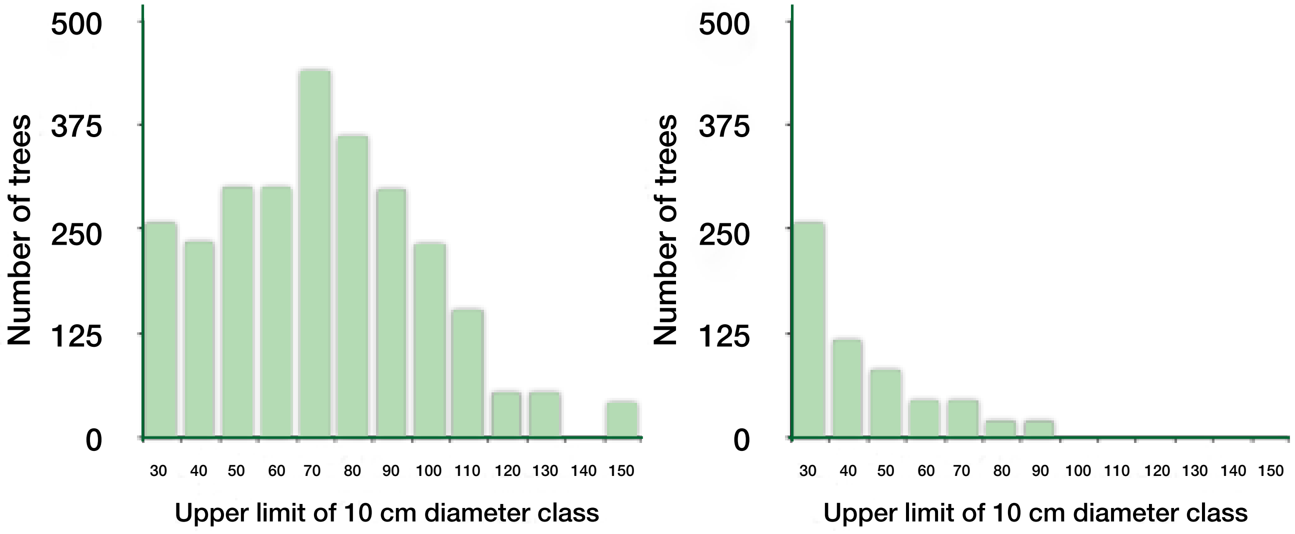

Figure 1. Estimated number of trees by diameter class before (left) and after (right) logging. Based on density/100 ha [Source: Grogan et al. (2008), extrapolated to the whole 4,100 ha area].

Genetics studies have shown that mahogany at Marajoara is only weakly genetically differentiated from neighbouring populations up to 100 km away.

Logging and management scenario

The Marajoara forest was logged between 1992 and 1994. Mahogany-rich areas of forest were first identified from the air. Subsequently, trees were located on the ground by specialized woodsmen. Felling was carried out in the wet season, followed by extraction during the dry season. Logging was typically done by teams of around 25 workers (employees of vertically integrated sawmills) using heavy machinery (bulldozers, skidders, road graders). These teams could fell more than 1000 mahogany trees in about 3 months.

More than 91% of trees above the then minimum legal cutting diameter (45 cm) were removed, as were 31% of trees in the 20–45 cm dbh range; the latter were felled illegally. In general, all trees found by specialized woodsmen were cut, on the assumption that parts of the upper stem of even rotten and poorly formed trees would yield merchantable timber. The number of trees per dbh class after logging is shown in Figure 1. Mean dbh after logging was about 41 cm. Smaller trees were more likely to be left because they were less likely to be found, rather than because of conscious selection of large trees.

Studies have detected significant impacts of logging at Marajoara on genetic diversity at the molecular level: measures of neutral (i.e. non-adaptive) diversity were higher in remnant trees than in their progeny, suggesting that logging has led to a reduction in the number of pollen and seed trees contributing to regeneration in any given part of Marajoara.

Post-2003 reforms

In 2003, a new regulatory framework for mahogany management was implemented in the Brazilian Amazon. Since 2003, loggers are obliged to carry out a complete inventory of the management area, reducing the likelihood of missing any trees of >20 cm dbh. Minimum cutting diameter was raised to 60 cm, and loggers are required to retain at least 20% of trees of >60 cm dbh, at a minimum density of five such trees per 100 ha. There are no restrictions on the form or health of these remaining trees.

Regeneration and management

The ecological considerations outlined above suggest that, without silvicultural intervention, remnant trees would be unlikely to produce any adult progeny. In this case, the question of any impact of dysgenic selection, which occurs in the following generation, would not arise. For this reason, we assume here that, during the same dry season that logged trees are extracted, an area of 0.5 ha is cleared (canopy opening) around each remnant tree with ≥25 capsules, and that the same area is then weeded annually for the next four years.

The exercise

Task 1: Discuss whether, in this logging operation, dysgenic selection would be likely to occur

Discuss the following questions:

- *Would the pre-2003 logging/management regime described above be likely to lead to dysgenic selection? For simplicity, you should assume that the logging operations from 1992 to 1994 were actually completed in one logging season.*
- *How might the logging reforms introduced in 2003 affect your conclusions?*
- *Use the framework provided by the breeders' equation to assist you. In doing so, you may find it useful to address the following questions:*
- *First, which trees are likely to be the progenitors of new, post-logging generations?*
- *Second, how inferior are these progenitor trees, in phenotypic terms and for which trait(s), in comparison to the trees of the population prior to logging?*
- *Third, to what degree will any such inferiority be inherited by their progeny?*

You may find that some of the data that you need to apply the breeders' equation may be lacking. In this case, you will need to make assumptions and also illustrate the sensitivity of your answer to these assumptions.

Task 2: Formulate a general set of risk factors that would suggest susceptibility to dysgenic selection

Prepare a diagram or table summarizing factors likely to increase the probability that a given logging event would lead to dysgenic selection. The factors might be ecological, genetic, socio-economic, related to specific details of harvesting practice or other issues. You should not necessarily restrict your analysis to timber trees.

In preparing your diagram or table, you may find it useful to consider the same three questions listed under Task 1, in relation to both the case study and possible scenarios in other species. One possible format is included below (although you are free to design your own):

Related process or characteristics	Risk factors	Explanations
Harvesting regime	Factor(s)	
Surrounding populations	Factor(s)	
Reproductive ecology (mating/seed/seedling)	Factor(s)	
Genetics	Factor(s)	

Task 3. Discuss the consequences of dysgenic selection and how it can be mitigated

Discuss and, if possible, reach agreement on the following two questions:

- *Is dysgenic selection a conservation genetics issue?*

The sorts of traits for which loggers select tend to be controlled by genes at many different loci, each of which has only a small effect on the phenotype. This implies that even strong selection on a particular trait translates into weak selection on any given locus. Given this, is dysgenic selection likely to lead to loss of alleles? How might your conclusion be altered in the case of selection on a trait with simple Mendelian inheritance?

- *How can dysgenic selection, should it occur, be mitigated or reversed?*

By definition, dysgenic selection, should it occur, leads to a decline in genetic quality of the population. Large effects could be catastrophic in terms of productivity and profitability. What measures could be taken to reduce or reverse the effects of dysgenic selection in a forest that had been heavily affected? How technically and institutionally feasible might they be?

Information sources

The case study is based on the work of a number of researchers, most notably Dr James Grogan (Yale University, Connecticut, USA, and Instituto do Homem e Meio Ambiente da Amazônia, Pará, Brazil) and his associates. This work is documented in the following publication and references therein:

Grogan J, Jennings SB, Landis RM, Schulze M, Baima AMV, Lopes J do CA, Norghauer JM, Oliveira LR, Pantoja F, Pinto D, M Silva JM, Vidal E, Zimmerman BL. 2008. What loggers leave behind: Impacts on big-leaf mahogany (Swietenia macrophylla) commercial populations and potential for post-logging recovery in the Brazilian Amazon. Forest Ecology and Management 255:269-281.

Forest Genetic Resources Training Guide

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1.2 *Talbotiella gentii*: genetic variation and conservation
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MODULE 5 How local is local? – the scale of adaptation
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Other modules to be published among the following:

Plantation forestry, Tree domestication, Forest restoration, Genetic modification