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

Jonathan Cornelius
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Module 4
Forest Management

Teacher’s notes 4.2

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

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Introduction

These Teacher’s notes aim to assist teachers in using Case Study 4.2 Dysgenic selection: can logging degrade the genetic quality of succeeding generations? in the classes. The notes:

• describe the key concepts covered in the case study, referring to forest genetics textbooks and other sources where explanations can be found (full references are given at the end of these notes)
• give tips on how to prepare and run the exercise and discuss the main learning points (genetic and other) that students should be able to derive from the case study
• outline the PowerPoint presentation, which introduces the case study to the students, and provides commentary the teacher can use (the presentation contains pictures of the species, sites where it occurs, relevant land-use issues in the area and figures/tables from the exercise)
• include an explanatory commentary on the case study document
• summarize key elements to be covered in the tasks.

The case study document is intended to be a stand-alone document, assuming that students are undergraduates or graduates in forestry (or in related disciplines). However, prior reading on basic quantitative genetics (polygenic traits, response to selection) might be advantageous (see, for example, Jansson 2005).

Support materials are provided on the accompanying DVD and are available on the Forest Genetic Resources Training Guide webpage at www.bioversityinternational.org

These include:
• The case study
• The Teacher’s notes
• The Teacher’s PowerPoint presentation.

Key concepts to cover/introduce in this case study

General conservation

Genetic concepts
• **Heritability and genetic gain**: see Jansson (2005); Walsh and Lynch (2008a; 2008b).

There is widespread perception of dysgenic\(^1\) selection as a threat to forest genetic resources, based on the belief that species or populations will degenerate if only the ‘worst individuals’ reproduce. However, this perception is largely the result of the simplicity and apparent reasonableness of the central belief rather than being based on experimental observations or study. Indeed, there are no proven examples of dysgenic selection having occurred, at least in the forestry sector, and the necessary conditions for it to occur in a forest management context appear to be rather stringent. This exercise aims to lead students towards this conclusion, while fulfilling two specific learning objectives:

• That the student should be able to identify situations in which dysgenic selection is likely to occur (or not occur)
• That the student should be able to explain to forest managers, certifying agencies and others why a given silvicultural regime might or might not lead to dysgenic selection.

As dysgenic selection is a form of phenotypic selection, the potential for dysgenic selection is explored using the framework of the ‘breeders’ equation.’ This equation encapsulates the theory of phenotypic selection on quantitative traits and facilitates a clear and logical presentation of the issues.

The case study includes background material on:
• the breeders’ equation
• mahogany ecology and genetics
• the mahogany-rich Marajoara site in Brazil.

### How to run the exercise

The exercise can be run in a number of ways, depending on the time available, size of the class and level of knowledge of the students. The approach described below corresponds to a three-hour block session, e.g. during a training course or university practical class. In each case, the exercise is likely to work best if students work in groups of three to five and no more than six. Teachers should distribute the case study document at least 48 hours before the scheduled session. Careful reading of the document will take up to one hour and should be completed before the class. Teachers and any assistants should be fully familiar with both the case study and these Teacher’s notes.

• **Introduction**: Begin the session by using the PowerPoint presentation to introduce the theme and the exercise (30 minutes). The presentation is intended as an overview and ‘appetizer,’ rather than as an exhaustive briefing. The table in Annex 1 describes the function of each slide and includes a commentary and notes that presenters may find useful. Teachers should encourage students to ask questions during the presentation rather than simply reciting the text to them. The text is also included on the notes panel of each slide.

• **Group work**: The group work focuses on three tasks: Task 1. To discuss whether, in this logging operation, dysgenic selection would be likely to occur (or not occur).

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\(^1\) Students may question whether “dysgenic” is a real word! The term dates from the early 20th century, and was initially used in the context of human societies and genetics. For example, the novelist Aldous Huxley referred to “dysgenics—the carrying on of the species by the worst members” - “Dysgenics” is the opposite of eugenics, i.e. selective breeding to improve the genetic quality of the human race, which was widely advocated in the late 19th and early 20th centuries, but has since been recognized as both unethical (at best) and based on dubious scientific assumptions. Neither term is derived directly from “gene”, which came into use later.
occur; Task 2. To formulate a general set of risk factors that would suggest susceptibility to dysgenic selection; Task 3. To discuss the consequences of dysgenic selection. Assign one of the three tasks to each group (but note that more advanced students may be able to cover Task 1 or 2 and Task 3). Students should discuss the case study amongst themselves, responding to the specific points and assigned tasks. The teacher should be present to answer questions (45 minutes discussion, 15 minutes to prepare presentations).

- **Presentations and teacher feedback:** Each group presents the outcomes of its work (10 minutes per presentation, with around 5 minutes after each presentation for questions and comments from the rest of the class and the teacher (based on five groups; more time can be allocated if there are fewer groups).

There are a number of alternative approaches to running the exercise. In the context of a training course, groups could be asked to reconvene to make their presentations the following day. In a university context, all three tasks could be assigned to each group as a take-home assessment task for completion over all or part of a one-semester course. In this case, one 50-minute lecture period could be devoted to the introduction and preliminary discussion.

**Notes and commentary by case study headings**

**Introduction**
This section introduces the concept of dysgenic selection, noting that the conditions under which it might occur are not as widespread as might be expected. It then states the tasks and learning objectives.

**Exploring dysgenic selection: response to selection and the ‘breeders’ equation’**
The breeders’ equation is used to predict response to selection. For this reason, it is important to explain clearly what we mean by the ‘response to selection.’ The approach taken here is to begin with realized response, as this is easily understood. We use an example from tree improvement because (a) tree improvement techniques may be familiar to some students and (b) there are no available examples of realized response to dysgenic selection. The idea that, just as tree improvement produces a positive response to selection, dysgenic selection produces a negative response has already been presented in the introduction and should be readily appreciated here.

Some students may struggle with the concept of response to selection as a genetic response because it is measured on phenotypic values. One way to deal with this is to explain that, at a given site, genetic and environmental deviations from the phenotypic mean would sum to zero and that therefore genetic and phenotypic means are identical. However, that concept would probably only be grasped readily by students who had already understood the initial point. A more effective approach would be to ask “what other factors could have caused the response?” and then, if necessary, point out why the approach to measuring the realized response in fact rules these out.

**The response to selection**
The general approach mentioned at the start of this section describes improvement from one generation to the next. Some students may notice that in the example given in Box 1 both seedlots come from the same generation. It may be necessary to point out that it is the improved progeny that would actually be carried forward to form a new generation. The “SSO [seedling seed orchard] routine” seedlot represents what would happen if the parental population were used to form a new generation without any selection being applied.
Predicting response: the breeders’ equation
This section introduces the breeders’ equation, providing a simple form of the equation before going on to discuss its application in subsequent subsections.

Selection differential
The selection differential (S) is commonly expressed in units of the phenotypic standard deviation, i.e. as the selection intensity. This approach has two advantages: (a) it permits direct comparison of the strength of selection in different traits, or in the same trait when populations have different standard deviations, and (b) under truncation selection (i.e. when all individuals to the right or left of a given point in a frequency distribution are selected), values can be derived from the proportion selected, assuming that values of the trait in question are normally distributed.

In spite of these advantages, we use the unstandardized selection differential here, i.e. expressed in terms of the measurement units rather than the standard deviation units of the selection intensity. We have chosen to do this because using selection intensity would add complexity (truncation selection, normal probability function, an extra term in the breeders’ equation). This is because selection intensity rests on a dubious assumption (normal distribution), and because it would give an erroneous impression that dysgenic selection is necessarily truncation selection. In any case, the selection differential is a more readily understandable measure of phenotypic superiority.

Students often confuse the selection differential with the response to selection. The key here is to stress that S is a phenotypic, within-generation difference, whereas response to selection (R) is a genetic and between-generation difference.

Heritability
Students frequently have problems with heritability concepts. The familiarity and the common use of the word ‘heritable’ cause problems; students may wrongly assume that, because they know the meaning of ‘heritable,’ they also know the meaning of ‘heritability.’ This misunderstanding should be addressed by ensuring that the students read the case study document carefully. In their interactions with individual groups, teachers may find it useful to introduce a parent–progeny regression concept of heritability, and/or the concept of heritability as the coefficient of determination in a regression of genotype and phenotype. However, both approaches assume additional knowledge and the teacher will need to assess whether the students possess such knowledge.

The breeders’ equation applied to dysgenic selection
The example used is hypothetical, partly to facilitate learning and partly to stimulate thinking about the factors that might mitigate apparent dysgenic selection in real situations.

Case study species and case study site and management regimes
These sections provide a reasonably complete account of the case study species, site and management regimes. The information provided is sufficient for the students to appreciate the context and to respond to the tasks. Not all the details included are needed to do the tasks; students will have to distinguish directly relevant information from less relevant data and background details to complete the tasks successfully.

Note that the scenario presented is based on logging at Marajoara, rather than being an exact case study. As is pointed out in the case study document, a ‘business-as-usual’ scenario would probably lead to zero regeneration. In that case, dysgenic selection would be unimportant.
Notes on the tasks

Task 1. Discuss whether, in this logging operation, dysgenic selection would be likely to occur
The best way to approach this question is by working backwards from hypothesized postlogging regeneration. You can guide the students by posing a number of questions, as follows:

Where will regeneration be found?
Postlogging regeneration is likely to be made up almost exclusively of seedlings in the cleared areas around remnant trees, as elsewhere most seedlings will be shaded out.

Which trees will be the seed parents of the regeneration?
Clearly, remnant trees will be the seed parents of all, or practically all, of the seedlings.

Which trees will be the pollen parents of the regeneration?
As mahogany trees are usually outcrossing (see ‘Ecology’ in the case study), remnant trees are unlikely to be both pollen parents and seed parents of seedlings in their immediate vicinity. Based on the information given under the heading ‘Regeneration and management’ in the case study, and assuming that the logging that occurred between 1992 and 1994 was completed in one season, there are six flowering events that could give rise to seed during the ‘regeneration window’ afforded by opening the canopy around the remnant mother trees: the first would occur in the dry season before felling, the second following felling, and then annually in the years corresponding to the four subsequent annual weedings. Logged trees could contribute to the first of these, but not to the others. Populations around Marajoara had already been heavily logged, so it is unlikely that a significant proportion of pollen parents in any of these six events came from trees in the original populations.

Given the expected parentage of the regeneration, what is the selection differential?
Some groups may choose to disregard the contribution of logged trees, as this would occur in just one of six flowering events. They could then proceed to calculate selection differential based only on the mean diameter at breast height (dbh) of remnant trees:

\[
S = \text{mean dbh of remnant trees} - \text{mean dbh before logging}
\]

\[S = 41 \text{ cm} - 67 \text{ cm} = -26 \text{ cm}.\]

Some groups may take other approaches. For example, the annual variation in fruit production mentioned in the case study may imply annual variation in flower production. So, if the dry season before felling (that is, the year in which logged trees would have been able to contribute as pollen parents) were a heavy-flowering year, then the influence of logged trees would be greater than if it were a year of little flowering. Furthermore, if the role of logged trees as pollen producers is to be taken into account, then groups might attempt to allow for differential contribution by different size classes. One approach would be to weight size classes crudely using the near four-fold greater fruit production of trees in the >60 cm dbh class (assuming proportionality of flower and fruit production).

The prelogging mean dbh of trees ≤60 cm dbh and >60 cm dbh was 40.6 cm and 83.6 cm respectively. There were 804 and 1609 stems respectively in these two broad size classes (values can be estimated from Figure 1 in the case study document). If trees in the >60 cm dbh group produce, on average, three times as much pollen as those in the ≤60 cm dbh group and they are approximately
twice as numerous, then in the calculation of weighted mean dbh of pollen parents contributing to postlogging regeneration in that year, the former would be accorded a weight six times as great as that of the latter:

$$[40.6 + (83.6)6]/7 = 77.46 \text{ cm}$$

Consequently, the selection differential for the same year would be:

$$S = \text{mean dbh of pollen and seed parents of next generation – unlogged population mean dbh}$$

$$S = (77.46 + 40.6)/2 - 67 \text{ cm} = 59.03 - 67 = -7.97 \text{ cm}$$

The overall selection differential applying to the future regeneration would be the mean over the six flowering events. One possible estimate of selection differential ($S = -20.0 \text{ cm}$) is shown in Table 1, in which it is assumed that two of the years (the first, to which logged trees contribute, and year 5) are heavy-flowering years in which flowering and fruiting are four times the long-term mean. Here, no within-year, between-size class weighting has been applied for the second and subsequent years, because after logging there is only one size class in the higher fertility group >60 cm dbh). Very ambitious groups might decide to tackle this issue by assuming some continuous relationship between size class and reproductive contribution, such that there are differences in reproductive contribution between the ≤60 cm dbh classes. Arguably, unlogged population mean dbh should also be calculated by weighting the contribution of different size classes; this would give higher values of the selection differential.

| Table 1. Illustration of calculation of average selection differential over six years |
|---------------------------------|-----|-----|-----|-----|-----|-----|
| Weighting factor for flowering$^2$ | Year 1$^1$ | Year 2 | Year 3 | Year 4 | Year 5 | Year 6 |
| Mean dbh of parents of regeneration$^3$ | 59.03 | 41   | 41   | 41   | 41   | 41   |
| Selection differential (cm) | −7.97 | −26  | −26  | −26  | −26  | −26  |
| Mean selection differential = $$[(r-7.97)(4) - 26 - 26 - 26 - (26)(4) - 26]/12 = -20.00 \text{ cm}$$ |

$^1$ Year 1 corresponds to the flowering season before felling.

$^2$ Assuming that trees produce on average four times as many fruits in heavy-flowering years as in normal years.

$^3$ Mean in Year 1 reflects contribution of subsequently logged trees, which have a higher mean and are assumed to have higher pollen production (see text).

**What are the likely heritability values?**

Following the calculation of selection differential, groups will need to make assumptions about the value of the heritability for growth traits, based on the comments in the ‘Heritability’ and ‘Genetics’ sections of the case study. Values less than or equal to 0.1 would appear most reasonable, as hinted at in the case study. Based on this, they should conclude that dysgenic selection is unlikely to be significant, principally because of low heritability values.

Teachers might also point out the implications of variation in fertility even between trees of similar dbh (even when, as is the case here, only trees that produce ≥25 capsules are considered). The implication is that in each size class relatively few trees actually make a significant reproductive contribution. This
Teacher's Notes 4.2 Does selective logging degrade the genetic quality of succeeding generations through dysgenic selection?

decreases the reliability of heritability as a guide to the relationship between phenotype and genotype. Consequently, the dysgenic response could be either lower (including zero) or greater than predicted.

How might the logging reforms introduced in 2003 affect your conclusions?

As far as dbh is concerned, the 2003 reforms should further reduce the likelihood of dysgenic effects. Assuming the new regime is adequately overseen, no trees ≤60 cm dbh would be logged and larger numbers of trees ≥60 cm dbh would be retained (i.e. around 205, based on five trees per 100 ha over the total area at Marajoara of 4100 ha). However, the lack of restrictions on the form of seed trees is likely to mean that these are the worst formed of the legally harvestable trees. These 205 seed trees about 17% of the remnant trees; the others (the 1000 trees that are <60 cm) are expected to be of average form (because they were left on size criteria), implying that around 17% (202/1205) of the remaining trees are likely to be poorly formed trees of relatively high average fertility (because they are relatively large). It is possible, therefore, that without further fine-tuning, the new regime might lead to an increased probability of dysgenic selection. However, further study would be needed before concluding that there is a major risk of this occurring.

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

A model answer is provided below (Figure 1). Some groups may arrive at something similar without any guidance beyond the template included in the case study document.

<table>
<thead>
<tr>
<th>PROCESS OR CHARACTERISTICS</th>
<th>RISK FACTORS</th>
<th>EXPLANATION</th>
</tr>
</thead>
<tbody>
<tr>
<td>HARVESTING REGIME</td>
<td>1. Remnant trees are strongly inferior in one or more phenotypic characteristic: logging not highly selective</td>
<td>The less selective the logging, the more likely loggers are to take everything but the worst. If remnant trees are not inferior, then there can be no dysgenic effect</td>
</tr>
<tr>
<td></td>
<td>2. Logging is large-scale, with many remnant trees; or multiple small-scale operations with similar logging criteria</td>
<td>With small numbers of selections, mean phenotype is a poor guide to mean genotype. However, small numbers of remnants implies unpredictability rather than absence of effects</td>
</tr>
<tr>
<td></td>
<td>3. Logging is carried out before flowering or before seed dispersal</td>
<td>No opportunity for logged trees to contribute to subsequent generations from “beyond the grave” (either through pollen or seed)</td>
</tr>
<tr>
<td>SURROUNDING POPULATIONS</td>
<td>4. No nearby populations of the same species, or only logged populations</td>
<td>No mitigating gene flow from unlogged populations</td>
</tr>
<tr>
<td></td>
<td>5. Logged species is a facultative or obligate selfer</td>
<td>All implying that future generations will be derived solely or very largely from remnant trees</td>
</tr>
<tr>
<td>REPRODUCTIVE ECOLOGY</td>
<td>6. There is little pollen flow (inter- or intrapopulation)</td>
<td>Implied that their contribution to future generations will not be outweighed by smaller numbers of non-inferior but more fertile trees</td>
</tr>
<tr>
<td></td>
<td>7. There is no seed bank or there is little advance regeneration</td>
<td></td>
</tr>
<tr>
<td></td>
<td>8. Logged trees do not coppice</td>
<td></td>
</tr>
<tr>
<td></td>
<td>9. Inferior remnant trees are highly fertile</td>
<td></td>
</tr>
<tr>
<td>GENETICS</td>
<td>10. Selected trait(s) has high genetic variation</td>
<td>In a highly variable population, the worst trees are likely to be more inferior than in a less variable population</td>
</tr>
<tr>
<td></td>
<td>11. Selected trait(s) moderately or strongly genetically controlled</td>
<td>In many cases, genetic control of commercial traits is weak. In such cases, dysgenic effects between successive generations will be negligible</td>
</tr>
<tr>
<td></td>
<td>12. Trait non-quantitative with simple Mendelian inheritance, little environmental effect on phenotype</td>
<td>Could produce strong dysgenic effects between successive generations. Possible example: destructive harvesting of aguaje palm</td>
</tr>
</tbody>
</table>

Figure 1. Risk factors for dysgenic selection, classified according to four classes of process or characteristics.
**Task 3. Discuss the consequences of dysgenic selection and how it can be mitigated**

*Is dysgenic selection a conservation genetics issue?*

The question is meant to be provocative. Nevertheless, in the case of quantitative traits, and given both that selection on any one locus is weak and that this is reduced still further by low heritabilities, changes in allele frequencies over a few generations are likely to be negligible. Although a large number of such negligible changes can have a perceptible effect on the mean value of the trait selected for, there is little chance of a given allele being lost due to selection, particularly at realistic levels of heritability and over the number of generations applicable in the case of long-lived organisms such as timber trees.

To say that dysgenic selection is not a conservation genetics issue would overstate the case, but at least in timber trees it appears likely to be of limited short-term importance. Its importance has probably been overstated in the past.

*If dysgenic selection occurs, how can it be mitigated or reversed?*

Groups should be thinking in terms of both management (given that most commercial traits are heavily influenced by environment as well as genetics) and genetic measures. Mitigation could be through silvicultural techniques such as thinning, pruning and fertilization that can be used to improve product quality and quantity. Positive selection could reverse dysgenic selection by being built into forest management regimes or by being implemented through supplemental planting with improved or ‘average’ stock. However, even such simple measures may be difficult to achieve where institutions (either executing or enforcing) are weak.

**Further information**

Cornelius JP, Navarro CM, Wightman KW, Ward SE. 2005. Is mahogany dysgenically selected? Environmental Conservation 32:129–139. (This is a useful reference for instructors, but should not be given to students until after completion of the exercise).


Annex 1. Summary of the audiovisual presentation

Table A1. Summary of the audiovisual presentation.

<table>
<thead>
<tr>
<th>Slide no./Title</th>
<th>Function</th>
<th>Suggested spoken text</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1/Dysgenic selection: can logging be a form of ‘negative genetic improvement’?</td>
<td>Introduces the theme.</td>
<td>There are various ways in which forest genetic resources can be degraded or destroyed. Today we will look at one of these: dysgenic selection. It is closely associated with harvesting and regeneration practices. We’ll define dysgenic selection in just a few moments. First however, let’s have a look at some harvesting practices, both current and historic.</td>
<td>A definition at this stage would be ‘over-weighty’ and is unnecessary. But do say that we will define it, as this raises expectations and interest (and makes it clear that definition is important). The content that follows should get students thinking in the right direction (if they are not already aware of the subject) and will lead up to a formal definition. If genetic drift has already been considered elsewhere, then it might be helpful to mention at the outset that dysgenic selection (DS) is a different form of genetic deterioration.</td>
</tr>
<tr>
<td>2/La Mosquitia, Honduras</td>
<td>Example of logging suggestive (superficially, perhaps) of DS.</td>
<td>Later in this case study we will be looking in some depth at a quite recent case of mahogany logging in the Marajoara Forest in the Brazilian Amazon. Now, though, let’s go back in time and a few thousand kilometres to the north, to the Caribbean coast of Honduras in Central America, part of an area known as La Mosquitia or, in English, the ‘Mosquito Coast.’ Inland of the lagoons and…</td>
<td>Forward to slide three on reaching the word “lagoons” in text. Figure from Von Hagen WV. 1940. The Mosquito Coast of Honduras and its inhabitants. Geographical Review 30:238–259.</td>
</tr>
<tr>
<td>3/‘Mahogany bush’</td>
<td>Example of logging suggestive (superficially, perhaps) of DS.</td>
<td>… and the Pinus caribaea savannah of the coast, can (or could) be found mahogany-rich areas of forest, which, by the 1940s, and probably long before, had attracted the attention of foreign logging companies.</td>
<td>Photos from Von Hagen WV. 1940 The Mosquito Coast of Honduras and its inhabitants. Geographical Review 30:238–259. See also Slide 32 (alternative).</td>
</tr>
<tr>
<td>Slide no./Title</td>
<td>Function</td>
<td>Suggested spoken text</td>
<td>Notes</td>
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</tr>
<tr>
<td>4/No title</td>
<td>Example of logging suggestive (superficially, perhaps) of DS.</td>
<td>Von Hagen (1940), writing in the Geographical Review, described a logging operation as a result of which, in his words “for the first time since 1900 the woods are coming to life again.” The company operating the concession would fell all commercially valuable mahogany trees (i.e. trees more than about 30 years old). These were floated to the mouth of the Caratasca Lagoon and from there were shipped to Florida. However, Von Hagen reported that regeneration of the forest was, nonetheless, assured.</td>
<td>The rich (unintended) irony is worth highlighting! Photo: Leonardo F Freitas, Pará, Brazil. Flona de Jamanxim Para. <a href="http://www.flickr.com/photos/leoffreitas/1469427761/sizes/m/">http://www.flickr.com/photos/leoffreitas/1469427761/sizes/m/</a></td>
</tr>
<tr>
<td>5/Regeneration assured?</td>
<td>The aim here is that students should themselves wonder whether susceptibility to termite attack could have some genetic basis.</td>
<td>[Read or paraphrase the quote from Von Hagen on the slide], then: ...so, the forest would be regenerated exclusively by those mahogany trees that had been infested by termites. Let’s now go south to the Amazon, but to the west rather than the east.</td>
<td>Questions or comments might be invited at this stage (particularly if an obvious ‘pregnant pause’ is made after “termites”), or might be raised anyway. Susceptibility of trees to attack by termites could perhaps be related to general vigour, which in turn would be expected to be influenced by genotype.</td>
</tr>
<tr>
<td>6/Iquitos, Peruvian Amazon</td>
<td>Leading into subtopic on aguaje palm.</td>
<td>Iquitos is a dynamic, bustling city in the Peruvian Amazon, in spite of having no road connections to the outside world. Many kinds of forest products can be found in the markets of Iquitos…</td>
<td>Forward to slide 7 on “markets of Iquitos...”</td>
</tr>
<tr>
<td>7/Medicinal species, Iquitos</td>
<td>Interest/variety, linking to the main subtopic.</td>
<td>...including medicinal species and…</td>
<td>Forward to slide 8 on the word “and” [This slide should last for about one second.]</td>
</tr>
<tr>
<td>8/Fruit species</td>
<td>Linking.</td>
<td>…of course, fruits, perhaps the most important of which is…</td>
<td>Forward to slide 9 on “of which is...” [This slide should last for about one second.]</td>
</tr>
<tr>
<td>9/The aguaje palm (Mauritia flexuosa)</td>
<td>Example of harvesting suggestive (superficially, perhaps) of DS. Mauritia flexuosa was selected to emphasize that concerns are not restricted to genetic resources of timber species.</td>
<td>... the aguaje palm, Mauritia flexuosa.</td>
<td></td>
</tr>
<tr>
<td>Slide no./Title</td>
<td>Function</td>
<td>Suggested spoken text</td>
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<tr>
<td>10/A major local industry</td>
<td>Linking through to the harvesting method.</td>
<td>In Iquitos a significant industry is built around the aguaje palm, giving employment to about 5000 people in different stages of the supply chain, including harvesters, middlemen, street-corner vendors, and manufacture and sale of processed products like this ice cream. Around 20 tonnes of aguaje fruits are consumed each day in the city. Our interest, though, is in the first stage of the supply chain.</td>
<td></td>
</tr>
<tr>
<td>11/Harvesting aguaje</td>
<td>Setting up the suggested dysgenic scenario.</td>
<td>Those 20 tonnes are equivalent to about 400 trees, which are felled to harvest the fruit. Around 1500 ha of aguaje—pure or almost pure stands—are felled each year. As the market prefers large fruit, trees with large fruit are preferentially felled. Felled trees do not coppice, and all their seed is collected.</td>
<td></td>
</tr>
<tr>
<td>12/Mauritia flexuosa types</td>
<td>The suggested DS scenario.</td>
<td>Fortunately, in one sense, the species is dioecious, so all the male trees are left, together with remnant females—escapees (those that did not produce fruit that year or that were 'missed' by the harvesters) or those with small fruit. The succeeding generation will be produced from these escapees and inferior trees. Another threat is low effective population size resulting from unequal sex ratios (as only females are felled). The two factors may also act synergistically.</td>
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<td>13/No title</td>
<td>Summing up and leading into the definition.</td>
<td>So, both these harvesting regimes have in common the possibility that only the 'worst' members of the population will reproduce... which brings us to our definition of dysgenic selection. &quot;Both&quot; refers to mahogany in Honduras and aguaje palm in Peru.</td>
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<td>14/Dysgenic selection</td>
<td>The definition.</td>
<td>Dysgenic selection is selection that leads to an undesirable directional change in genetic quality over one or more generations. By 'genetic quality' we usually mean performance for a given commercially important trait (such as growth rate or survival), and by 'directional change' we mean a positive or negative change in mean values. Directionality distinguishes dysgenic selection from genetic drift, which can also lead to undesirable changes in genetic quality, but in a random way and in another sense (i.e. random loss of alleles). The instructor should consider asking for definitions of both 'genetic quality' and 'directional,' and asking how directional differs from random drift (or, for that matter, 'genetic contamination' through gene flow).</td>
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<td>15/Claims of dysgenic selection and variation patterns'</td>
<td>Pointing out that the risks have been suggested in the literature: the theme is 'on the agenda.'</td>
<td>It has been suggested a number of times that dysgenic selection might be of importance in forest trees. For example, Palmberg suggested that it could explain why provenance variation in two Mediterranean pine species failed to show relationships with latitude or longitude. Palmberg C. 1975. Geographic variation and early growth in south-eastern semi-arid Australia of Pinus halapensis Mill. and the P. brutia Ten. species complex. Silvae Genetica 24: 150–160.</td>
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<td>16/Claims of dysgenic selection and selective logging</td>
<td>Pointing out that the risks have been suggested in the literature: the theme is 'on the agenda.'</td>
<td>Similarly, it has been claimed that the poor form of the Caribbean mahogany, <em>Swietenia mahagoni</em>, is the result of the same factor.…</td>
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<td>17/Claims of dysgenic selection and selective logging</td>
<td>Pointing out that the risks have been suggested in the literature: the theme is 'on the agenda.'</td>
<td>...while, turning from possible pasts to possible futures, Lemes et al. suggested that this might still be happening in the case of <em>Swietenia macrophylla</em>. We have of course been hinting at such processes with the two examples of La Mosquitia and Iquitos. However, to clarify these ideas a little we need to look carefully at the term 'selective logging.'</td>
<td>Lemes MR, Gribel R, Proctor J, Grattapaglia D. 2003. Population genetic structure of mahogany (<em>Swietenia macrophylla</em> King, Meliaceae) across the Brazilian Amazon, based on variation at microsatellite loci: implications for conservation. <em>Molecular Ecology</em> 12: 2875–2883.</td>
</tr>
<tr>
<td>18/What is selective logging?</td>
<td>Aims to clarify the meaning, particularly to avoid the idea that, within species, it means 'high grading.'</td>
<td>‘Selective logging’ refers, of course, to the felling and extraction of only certain types of trees. However, for our purposes, it is useful to distinguish two slightly different types of selection as practised by loggers and other harvesters of forest products. First, we have the selective logging of particular species. Typically, loggers only extract those species that have commercial value, and this is the usual meaning of 'selective logging' when used in forestry.</td>
<td>Photo: Leonardo F. Freitas. Feliz Natal, Mato Grosso, Brazil. <a href="http://www.flickr.com/photos/leoffreitas/790041598/sizes/m/in/set-72157600605933144/">http://www.flickr.com/photos/leoffreitas/790041598/sizes/m/in/set-72157600605933144/</a></td>
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<tr>
<td>19/Within-species selective logging</td>
<td>Aims to clarify the meaning, particularly to avoid the idea that, within species, it means 'high grading.'</td>
<td>Second, we have selection within species. In this case, loggers don’t usually select 'only the best' (as the quote in slide 17 seems to suggest). Rather, they fell everything that it is worthwhile to fell, and therefore leave only the worst. In fact, if loggers took only the very best, then dysgenic selection would not be a serious worry. It would be like trying to carry out genetic improvement by letting all individuals reproduce except the very worst. This would not work, because genetic improvement by removal of just the very worst would have a negligible effect on the frequency in the population of the best alleles.</td>
<td>Photo: Leonardo F. Freitas. Senador Jose Porfirio, Pará, Brazil. <a href="http://www.flickr.com/photos/leoffreitas/447616048/sizes/m/in/set-72157600605933144/">http://www.flickr.com/photos/leoffreitas/447616048/sizes/m/in/set-72157600605933144/</a></td>
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<td>20/Dysgenic selection: the mirror image of genetic improvement</td>
<td>Linking back to DS as the opposite of genetic improvement.</td>
<td>In genetic improvement, breeders often select the very best and allow only those individuals to reproduce. In logging, loggers often leave only the very worst, and these ‘selected individuals’ (which of course are those left by loggers, rather than those selected by them) are those that reproduce and give rise to the next generation. So dysgenic selection is like the mirror image of genetic improvement...</td>
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<td>21/Positive phenotypic selection aiming at genetic improvement</td>
<td>Consolidating the ‘mirror image idea’ and leading into explicit cases of negative and positive selection.</td>
<td>...and we can illustrate that with these data from a Vochysia guatemalensis plantation in Sarapiquí, Costa Rica... [briefly explain what the graph shows] In this case, we’re illustrating positive phenotypic selection. Trees above 7 cm dbh have been selected, and eventually only these will be allowed to reproduce.</td>
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<td>22/Negative phenotypic selection, possibly leading to dysgenic selection</td>
<td>Negative selection.</td>
<td>In this case, we are imagining the selection of only those trees with dbh &lt; 2 cm. If only these 35 or so small trees were allowed to reproduce, then there would be a risk of dysgenic selection.</td>
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<td>23/There are no documented examples of dysgenic selection in forest trees</td>
<td>Leading in to the need for prediction and the breeders’ equation.</td>
<td>In fact, there are no documented examples of dysgenic selection actually having happened in forest trees. This should not be seen as an indication that it is not important—rather, it reflects the fact that no one has seriously looked into it. For example, no one has ever compared the growth rate of progeny of logged and remnant trees. As a result, we need to approach this subject from a theoretical viewpoint. Fortunately, as dysgenic selection is like genetic improvement in reverse, the highly successful theory that underlies genetic improvement serves as our framework. Much of this framework is summarized in one relationship, known as...</td>
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<td>24/The breeders’ equation</td>
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<td>...the breeders’ equation, which allows us to predict the effect of selection, whether positive (improvement) or negative (dysgenic). Let's look briefly at the three components.</td>
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### Slide 25: The breeders’ equation

**Response to selection (R) = selection differential (S) \times heritability (h^2)**

- **Function:** Explains the response to selection—what it is that we are trying to predict.

- **Suggested spoken text:**
  
  The effect of selection is quantified by the response to selection, which measures the change in performance between one generation (the one in which selection is carried out) and the next (the improved [or dysgenic] generation). It is measured in whatever units are appropriate to the trait being selected (e.g. dbh—cm, height—m, stem quality-score, density—kg/m^3), or can be expressed as a percentage. For example, if we select plus-trees in plantations, and trees grown from their seed grow 10% more quickly than average seed from the same plantations, then the response to selection is 10%.

- **Notes:**
  
  But before we carry out selection, we will not know its future impact, which is why we need to predict it. We do so using two parameters.

### Slide 26: The breeders’ equation

**Response to selection (R) = selection differential (S) \times heritability (h^2)**

- **Function:** Explains the selection differential.

- **Suggested spoken text:**
  
  First, let’s look at the selection differential, which is the difference between the selected individuals and the overall mean. For example, in the case just mentioned, if the plus-trees had a mean dbh of 40 cm and the population mean is 20 cm, then the selection differential is 20 cm. In itself, the selection differential tells us nothing about whether the superiority it expresses is due to genetics or some other cause—it is just a within-generation measure of difference.

### Slide 27: The breeders’ equation

**Response to selection (R) = selection differential (S) \times heritability (h^2)**

- **Function:** Introduces heritability.

- **Suggested spoken text:**
  
  Second, we look at the heritability, which measures the degree to which the superiority measured in the selection differential is passed on to the progeny. The value of heritability varies from zero to one—a typical value for dbh might be around 0.2. Putting these two together, we can predict the response to selection.

### Slide 28: The breeders’ equation

**Response to selection (R) = selection differential (S) \times heritability (h^2)**

- **Function:** Example of prediction of response to selection.

- **Suggested spoken text:**
  
  The heritability tells us that 20% of the phenotypic superiority expressed in the selection differential is due to heritable genetic characteristics (alleles that the plus-trees have). We therefore predict a between-generation genetic response of 20% of the selection differential, i.e. 4 cm.
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<td>29/Mahogany logging in Brazil</td>
<td>Finishing with the challenge posed by the exercise, which involves applying the breeders’ equation.</td>
<td>In our exercise, we will use this framework to explore both the nature of dysgenic selection and the probability of it occurring in a specific example based on logging in the Marajoara Forest, Pará State, Brazil. Marajoara is a 4100 ha industry-managed forest area, and is probably the most studied mahogany-rich forest anywhere.</td>
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<td>30/Marajoara before logging</td>
<td></td>
<td>Here is the distribution of dbh at Marajoara before logging...</td>
<td>The graph actually shows values for the sampled area at Marajoara, extrapolated over the entire 4100 ha, on the assumption of equal stocking throughout.</td>
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<td>31/Marajoara before logging...Marajoara after logging</td>
<td>Leads into the rest of the session (case study).</td>
<td>...and here is the dbh distribution after logging. Will the “continuous exploitation of large, superior individuals” lead to dysgenic selection, as suggested by some researchers? One of your tasks is to answer this question!</td>
<td>The two graphs are quite striking and should arouse interest. Draw attention to the obvious demographic impact of the logging, if it is not clear whether this has already been noticed.</td>
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Forest Genetic Resources
Training Guide

MODULE 1 Species conservation strategies
1.1 *Leucaena salvadorensis*: genetic variation and conservation
1.2 *Talbotiella gentii*: genetic variation and conservation
1.3 *Shorea lumutensis*: genetic variation and conservation

MODULE 2 Trees outside of forests
2.1 Conservation of tree species diversity in cocoa agroforests in Nigeria
2.2 Devising options for conservation of two tree species outside of forests

MODULE 3 Tree seed supply chains
3.1 Genetic bottlenecks in the restoration of *Araucaria nemorosa*
3.2 Tree planting on farms in East Africa: how to ensure genetic diversity?

MODULE 4 Forest management
4.1 Impacts of selective logging on the genetic diversity of two Amazonian timber species
4.2 Does selective logging degrade the genetic quality of succeeding generations through dysgenic selection?
4.3 Conserving *Prunus africana*: spatial analysis of genetic diversity for non-timber forest product management

MODULE 5 How local is local? – the scale of adaptation
5.1 Selecting planting material for forest restoration in the Pacific north-west of the USA
5.2 Local adaptation and forest restoration in Western Australia

Other modules to be published among the following:
Plantation forestry, Tree domestication, Forest restoration, Genetic modification