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# Introduction

The purpose of this document is to describe the LANDIS model for two groups of readers:

* **Software developers** who need to understand LANDIS conceptually, as a computational model, in order to do their job effectively. It is assumed that a developer reading this document already has some basic knowledge about computer simulation modeling (for example, the concept of state variables). However, some aspects of the model which are important to ecologists – such as the scientific justification for selecting particular algorithms – are not necessary for the developers’ understanding, and therefore are omitted. For more scientific information about the model, see the list of publications at the LANDIS-II web site:   
  www.landis-ii.org/site/landismodel/publications.
* **Ecologists** who want to learn about the LANDIS conceptual model without being encumbered by information related to implementing the model as computer software. Therefore, this document omits specific implementation details such as the format of data files. For that type of information, see the other documents in the set that describes the project’s software requirements.

## Notation

### Random Numbers

Because LANDIS model is stochastic, it uses random numbers. Random numbers are generated with different distributions. Each distribution is described by a set of parameters. For example, a uniform distribution has lower and upper bounds. The general notation for a randomly-generated number is:

random*Distribution Abbreviation* (*distribution parameters)*

The notation for a uniformly-distributed random number is:

random U( *lower bound, upper bound )*

The notation for a random number with an exponential distribution is:

random E( *mean )*

## References

The primary reference for the LANDIS-II model is:

Scheller, R.M., J.B. Domingo, B.R. Sturtevant, J.S. Williams, A. Rudy, D.J. Mladenoff, and E.J. Gustafson. 2007. Introducing LANDIS-II: design and development of a collaborative landscape simulation model with flexible spatial and temporal scales. Ecological Modelling 201 (3-4): 409-419.

LANDIS-II owes much to the developers of its scientific principles since it was introduced in 1996. Below is a partial list of these foundational LANDIS papers:

Gustafson, E. J., S. R. Shifley, D. J. Mladenoff , K. K. Nimerfro, and H. S. He. 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. Canadian Journal of Forest Research **30**: 32-43.

He, H. S. and D. J. Mladenoff. 1999. Spatially explicit and stochastic simulation of forest landscape fire disturbance and succession. Ecology **80**: 81-99.

Mladenoff, D. J., G. E. Host, J. Boeder, and T. R. Crow. 1996. LANDIS: A spatial model of forest landscape disturbance, succession, and management. Pages 175-179 *in* M. F. Goodchild, L. T. Steyaert, B. O. Parks, C. A. Johnston, D. Maidment, M. Crane, and S. Glendinning, editors. GIS and environmental modeling: progress and research issues. GIS World Books, Fort Collins, Colorado, USA.

## Acknowledgements

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# Overview

LANDIS-II is a forest landscape simulation model. It simulates how ecological processes including succession, seed dispersal, disturbances, and climate change affect a forested landscape over time (Figure 1).

Some processes are always active in a simulation run, for example, succession. Other processes such as disturbances are optional, so the modeler selects which of these processes are active during a simulation run.

Succession

Harvest

Landscape

Fire

Wind

Figure 1 – Ecological processes modify landscape.

## Process Time Steps

Each ecological process operates on its own individual time step (units: year). For example, fire may operate at a 3 year time step, while harvesting occurs at a 10 year time step. The time steps of any two processes may be the same, or they may be different.

# Landscape

The landscape is represented as 2-dimensional grid of equal-sized squares called **sites** or **cells**. An individual site is identified by its location – row and column – in the grid (Figure 2).

1,1

2,1

3,1

x,1

R,1

1,2

2,2

3,2

x,2

R,2

1,3

2,3

3,3

x,3

R,3

1,y

2,y

3,y

x,y

R,y

1,C

2,C

3,C

x,C

R,C

Figure 2 – Sites and their locations on the landscape grid.

## Region of Interest

Since the region of interest to the modeler is seldom rectangular in shape, a subset of the landscape’s sites is **active** during a simulation. Sites outside the region of interest are considered inactive. Also some sites within the region may be inactive because they represent locations where forests do not grow (for example, bodies of water, urban areas). See Figure 3.

active

inactive

water  
(in region,  
 but inactive)

Figure 3 – Region of interest on a landscape.

## Forest Sites

One or more tree species may be present on a **forest site**. Also, a site may be bare and have no species present at times during a simulation.

### Tree Species – Parameters

The model uses life history parameters that vary among tree species (Table 1). The model requires a small suite of life history parameters that are the most commonly required. Individual disturbance processes may require additional species-specific parameters. These additional disturbance-related parameters are described in the documents about specific types of disturbances (e.g., *LANDIS-II Base Wind*, *LANDIS-II Base Fire*, etc.).

Table – Parameters for Tree Species

|  |  |
| --- | --- |
| Parameter | Units |
| Name |  |
| Longevity | years |
| sexual maturity | years |
| shade tolerance |  |
| seed dispersal |  |
| effective distance | meters |
| maximum distance | meters |
| resprouting (vegetative reproduction) |  |
| minimum age | years |
| maximum age | years |
| probability of resprouting |  |
| post-fire regeneration |  |

### Tree species – Cohorts

For each species present on a forest site, the trees are grouped into **age classes**. An age class is a range of ages. The **span** of an age class is the size of the range, i.e., the number of years in the range. By default, the span for an age class is equal to the succession time step ∆tS (see section 4.1 *Succession Time* Step). For example, if ∆tS is 10 years, then the age classes would be 1 to 10, 11-20, 21-30, and so on.

An age class is referred to by its upper bound on its range. For example, the age class 11 to 20 would be referred to as age class 20 or simply, age 20.

For a species, each age class that is present on a forest site is represented by a **cohort**. Figure 4 shows a sample set of cohorts for a site with four species present; ∆tS is 10 years in this example.

Balsam fir

40

Sugar maple

250

White pine

Hemlock

10

20

100

150

200

10

80

90

190

270

290

Figure 4 – Example of a set of cohorts for a set (based on Table 1 in He1999).

### Shade

The amount of shade on a forest site plays a very important role in succession: it affects the ability of tree species to reproduce via seeding and resprouting (sections 4.5.1 and 4.5.2). A shade’s site is represented by an integer in the range of 0 (none) to 5 (most).

## Landscape Initialization

At the beginning of a model run, the landscape’s sites are initialized from a **site initialization map**. This map assigns each active site to an initial site class. The definition of each site class specifies the tree species that are present on each site in the class along with the particular age classes that are present for each of those species (Figure 5).

1

2

4

3

1

1

1

1

1

1

1

1

1

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1

1

1

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1

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**Initial Site Classes**

Class Species & Ages

1 basswood: 10, 20

sugar maple: 20, 40, 50

hemlock: 120, 250, 300

2 sugar maple: 20, 40, 50

hemlock: 120, 250, 300

3 (none – water)

4 yellow birch : 20, 60, 100

hemlock: 310

Figure 5 – Example of a site initialization map.

## Ecoregions

The modeler provides an input map which divides the landscape into ecologically defined **land types**. These land types are also called **ecoregions** in broad scale studies. Sites with similar ecological conditions are grouped into a single land type. Because these conditions or factors affect ecological processes such as succession and disturbances, a site’s land type influences the effect these processes have on the site. This influence is represented in the model as land type parameters. For example, the effect of land type on a species’ ability to establish is represented by a **species establishment coefficient** (Table 2).

Table – Parameters for Land Types (Ecoregions)

|  |  |  |
| --- | --- | --- |
| Parameter | Data Type | Units |
| name | String |  |
| establishment coefficient species | 0 ≤ number ≤ 1 |  |

If a land type does not have an explicit establishment coefficient for a particular species, a coefficient of 0 is implied (i.e., the species cannot establish in that land type). A land type may have no establishment coefficients for any species because it represents a region of the landscape which does not have forested sites (for example, bodies of water, urban areas).

# Succession

## Time Step

The succession time step, ∆tS, is specified by the modeler, and may differ between simulation runs. The time step determines the span of the age classes for the tree species cohort (section 3.2.2).

## Stages

Succession involves these 3 stages:

1. cohort ageing and mortality (senescence) (section 4.3)
2. computing shade for forest sites (section 3.2.3)
3. cohort reproduction by seeding and resprouting (sections 4.5.1 and 4.5.2)

## Interaction with Other Processes

The set of sites that undergo succession for a particular time step is based on whether that time step is also a disturbance time step:

* If the current time step is just a succession time step and not a disturbance time step, then all the forest sites on the landscape undergo succession.
* If the current time step is both a succession time step and a disturbance time step, then only those forest sites not disturbed during the current time step undergo succession.

## Cohort Ageing and Mortality

In this stage, the tree species cohorts of the selected sites are updated for cohort ageing and mortality.

### Ageing

The age of a cohort at a site is updated as follows:

age( t ) = age( t AM ) + ( t – t AM )

where

t is current model time step, and

t AM is the time step that cohort ageing & mortality was last done for the site.

The ageing of **young cohorts** is handled differently. A young cohort is one whose age is less than the succession timestep:

age( tS ) < ∆tS 🡪 young cohort

If the current time step is a succession time step, then the age of a young cohort is updated by setting it to the succession time step. However, cohort ageing and mortality also occur during a disturbance time step. In the case where the current time step is just a disturbance time step and not a succession time step, the age of a young cohort is updated in the same manner as other cohorts:

∆tS, if t is a succession time step

young cohort 🡪 age( t ) =

age( t AM ) + ( t – t AM )

If one or more disturbance processes are active during a run, it is possible for a species to have two or more young cohorts with different ages depending upon the succession and disturbance time steps involved. When a species at a site has 2 or more young cohorts during the ageing stage of a succession time step, the young cohorts are combined into a single cohort with its age equal to the succession time step. The following example illustrates this behavior:

*Example*: ∆tS = 10 years, ∆t wind = 5 years. At year 30, a species seeds a site, resulting in a new cohort with an initial age of 1 (section 4.5.6). Five years later, windthrow hits the site, causing the species to resprout and the addition of a new cohort.

Time Step Site Cohorts

year 30 – start of time step *species*: 100

– after succession *species*: 1, 100

year 35 – start of time step *species*: 1, 100

– after wind kills old cohort *species*: 1

– after ageing & mortality *species*: 6

– after resprouting *species*: 1, 6

year 40 – before ageing *species*: 1, 6

– after ageing *species*: 10

### Mortality (Senescence)

A cohort’s updated age is compared with the longevity of the cohort’s species; if the age exceeds the longevity, then the cohort “dies”, and is removed from the site.

age( t ) > longevity species 🡪 cohort removed

Typically, a species’ maximum age for resprouting is less than the species’ longevity. However, if these two parameters are equal for a species, the death of one of that species’ cohorts may trigger resprouting (section 4.5.2).

## Cohort Reproduction

Tree species reproduce in the following ways:

* Dispersing seeds
* Resprouting (Vegetation reproduction)
* Planting

The reproductive methods are associated with different ecological processes, for example, seeding with succession, planting with harvesting.

### Seeding

In this form of reproduction, a species reproduces from seeds. All seed dispersal operate in a similar fashion, although the specific formulae for calculating the seed dispersal probability distribution may vary. Each species has an effective and maximum seeding distance. Maximum is always greater than effective distance. Each species is processed separately. There are multiple algorithms for seed dispersal. A typical seed dispersal algorithm follows these steps:

1. First, conditions are checked to see if the seed can germinate (section 4.5.5 *Light Requirements*) and establish itself on the site (section 4.5.6 *Establishment*). If so, seeding is attempted for the site.

2. Seeds go *into* a site. Seeds do not propagate out into the surrounding matrix. Rather, for each site, neighboring sites are searched for seed sources.

3. A neighboring site can serve as a seed source if: a) at least one cohort of the same species at the neighboring site is older than the age of maturity and, b) the distance of the neighboring site from the site being processed is <= (maximum distance + cell size).

4. A probability of seed arrival is calculated based on the effective and maximum distances. These formulae vary widely.

5. Neighboring sites, as defined by the maximum distance, are searched until the probability of seed arrival exceeds a random number. At this point, all three criteria for reproduction (light, establishment, seeds) have been met and seed dispersal ends. Alternatively, seed dispersal will end when all neighboring sites have been checked.

The initial default seed dispersal algorithm will use **Brendan Ward’s** algorithm where two negative exponential distribution are used to calculate the probability of a seed landing at a site. The algorithm is scale-robust, meaning that the distribution is sensitive to changes in cell sizes, and represents a true probability distribution with leptokurtotic behavior.

In addition, two non-spatial seeding (not seed dispersal) algorithms are provided:

* **no dispersal** – no species can seed a neighboring site.
* **universal dispersal** – every species can seed any forest site on the landscape; a species does not need to even be present in any neighboring site.

### Resprouting

This form of reproduction (also known as **vegetation reproduction**) occurs when a species cohort dies. In order for the species to resprout, all these conditions must be satisfied:

1. The age of the cohort is in the species’ age range for resprouting (section 3.2.1 *Tree Species – Parameters*).
2. There is sufficient light (section 4.5.5 *Light Requirements*).
3. The species’ probability of resprouting (section 3.2.1 *Tree Species – Parameters*) exceeds a uniform random number between 0 and 1.

reprouting probability species > random U(0, 1)

A new random number is generated each time this condition is checked.

If a species establishes via resprouting on a site at a particular time step, no species can reproduce on that site by seeding for that time step.

### Planting

This form of reproduction occurs during harvesting. When a species is planted on a site, it is checked to see if the probability of establishment is greater than zero. If at least one species is planted on a site at a particular time step, no species can reproduce on that site by seeding or resprouting for that time step.

### Post-fire Regeneration (including Serotiny)

Regeneration following a fire can take one of two forms: resprouting or serotiny. If a species can resprout following a fire, it will follow the general rules for resprouting (section 4.5.2). If the species is serotinous (cones are opened by the heat of a fire), then the species will seed on site, following the general rules for seeding (section 4.5.1).

### Light Requirements

In order for a species to seed a site or to resprout on a site, there must be sufficient light. Sufficient light is determined by comparing the species’ shade tolerance with the shade on the site. The default algorithm is as follows:

shade tolerance species ≤ 4, and  
shade tolerance species > shade site

light is sufficient if or

shade tolerance species = 5, and  
shade site > 1.

However note that most succession extensions over-write this algorithm with an extension-specific equation.

### Establishment

To determine if a species that has reproduced on a site through seeding (or serotiny) establishes itself, the species’ establishment coefficient (EC) is compared with a uniform random number between 0 and 1. The EC is based on the site’s land type. A new random number is generated each time this establishment test is done. If the random number is less than the EC, the species establishes itself on the site.

random U(0, 1) < EC species, land type 🡪 species establishes

When a species establishes on a site, a new cohort for the species is created. The age of the new cohort is 1.

Note that this establishment test does not apply to reproduction by means of planting or resprouting. However, planting is subject to the constraint that EC must be > 0. Resprouting is not impacted by EC because it is assumed that the mature cohort being removed, which triggers the resprouting, is sufficiently established to support the new cohort.

# Disturbances

The modeler specifies which disturbance processes are active for a run. It is acceptable to have no disturbance processes active during a run.

## Timestep

Each disturbance process has its own timestep, ∆t *disturbance* , for example, ∆t fire or ∆t wind . This timestep may be the same as other disturbance processes, or may be the same as the succession timestep (section 4.1).

## Stages

In general, a disturbance involves these stages:

1. determine which forest sites are disturbed
2. modify the selected sites
3. do cohort ageing and mortality at the disturbed sites (section 4.3)
4. compute shade for the disturbed sites (section 3.2.3)
5. do cohort reproduction (the form of reproduction is based on the disturbance’s type)

## Multiple Processes at a Time Step

If two disturbance processes occur at a particular time step, then each process modifies sites – stages (a) and (b) – in the order specified by the user (section 5.3.1). The remaining stages – cohort ageing, mortality, and reproduction – are done just once after all the disturbances.

### Order

The modeler may specify the order in which disturbance processes affect the landscape. She may explicitly order the different disturbances (for example, fire first, then wind), or she may indicate that the order is random. In the latter case, a random order is generated for each time step where two or more disturbance processes affect the landscape.