

LANDIS-II Browse Disturbance v1.0 Extension User Guide

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1 Introduction

This document describes the **Browse Disturbance (v1.0)** extension for the LANDIS-II model. For information about the LANDIS-II model and its core concepts including succession, see the *LANDIS-II Conceptual Model Description*. The Browse Disturbance extension is designed to run with any succession extensions that carry cohort biomass attributes (e.g., Biomass Succession, PnET-Succession, NECN Succession).

The Browse Disturbance v1.0 extension is designed to simulate the removal of biomass from tree cohorts by ungulate browsers, and the concurrent loss of growth and/or mortality.

1.1 Major Releases

1.1.1 1.0 (September 2021)

Now compatible with Core v7 and does not require a special version of succession extensions.

1.2 Minor Releases

1.2.1 1.1 (December 27, 2021)

Now compatible with NECN Succession. Previously, the Browse extension required ecoregion-level Maximum Biomass values for each species, which it received from Biomass Succession. To make the Biomass Browse extension compatible with more succession extensions, Biomass Browse now requires a Maximum Biomass value to be given for each species.

1.2.2 Beta 0.8 (July 30, 2015)

- Bug fix in the neighborhood calculation of SitePreference for HSI calculation.
- Multiplied HSI values by 100 for map output.

1.2.3 Beta 0.7 (July 28, 2015)

- Defined EffectivePopulation as the minimum of zone population and zone carrying capacity (K).
- Added fields to log file, including TotalForage(kg), K, EffectivePopulation, BiomassRemoved(g/m²) and BiomassMortality(g/m²). The last 2 columns used to be lumped into one value labeled BiomassRemoved. The following columns of BiomassRemoved by species still represent a combination of browsing consumption and mortality.
- Changed units of the population output map to #/km² * 100. To convert this to a per cell population (given 100x100m cell) you would divide by 10000. Summing the cell values and converting the units should result in the same value as the EffectivePopulation reported in the log file (give or take small rounding errors).

- Bug fixes to the accounting of browse removal. There were some inconsistencies that mostly affected sites when browse levels were high (second pass removals), and resulted in less removal than should have been applied.

1.2.4 Beta 0.6 (May 27, 2015)

Bug fix related to the implementation of the “UseInitBiomassAsForage”. This option was not functioning previously and behaved as if always set to TRUE.

1.3 Acknowledgments

Funding for the development of the Browse Disturbance Extension has been provided by the Northern Research Station (Irvine, PA) of the U.S. Forest Service and the USGS ecosystems program. Valuable contributions to the development of the model and extensions were made by Patrick Drohan (Penn State University), Susan Stout, Alex Royo, Brian Miranda, Brian Sturtevant, Eric Gustafson (USFS Northern Research Station), Nathan De Jager (USGS Upper Midwest Environmental Sciences Center)

Funding for the development of LANDIS-II was provided by the Northern Research Station (Rhinelander, Wisconsin) of the U.S. Forest Service. Valuable contributions to the development of LANDIS-II were made by Robert M. Scheller, Brian R. Sturtevant, Eric J. Gustafson, and David J. Mladenoff.

2 Browse Disturbance Extension

Herbivory can exert significant control over plant community composition and ecosystem processes (Janzen 1970, Pastor et al. 1988, Rooney and Waller 2003). White-tailed deer (*Odocoileus virginianus*) browsing impacts on forest plant and animal communities derive primarily from defoliation and potential elimination of the shrub and seedling strata (Horsley and Marquis 1983, Liang and Seagle 2002, Horsley et al. 2003, Stout et al. 2014). Given the scale and magnitude of these impacts, white-tailed deer are now often classed as a keystone species in eastern North American forests (McShea and Rappole 1992, McShea and Schwede 1993) and have been suggested to create alternative stable states of woody-plant community composition (Stromayer and Warren 1997, Horsley et al. 2003; Royo et al. 2010). Similar ecosystem impacts have been documented for other forest ungulates, including moose (*Alces alces*) (Pastor et al. 1988, McInnes et al. 1992, Speed et al. 2013) and elk (*Cervus canadensis*) (e.g., Kaye et al. 2005). Such impacts have the potential to create feedback that may potentially change the density of ungulate populations in dynamic plant-herbivore systems (Coughenour and Singer 1996; Moen et al. 1998,).

The purpose of the Browse Disturbance extension is to reduce the growth and increase the likelihood of mortality for existing established cohorts according to a combination of published food preferences, variable ungulate abundance in time and space with the degree of realism defined by the user, and spatial factors affecting browsing pressure. The general approach to modeling browse disturbance on forests is to define available forage (annual growth of cohorts accessible to browsers) based on species preference and the composition of cohorts on each site (cell), remove some proportion of cohort biomass based on browser abundance and their preference for different species cohorts, and to impact susceptible species cohorts according to their ability to compensate for lost biomass. In addition, the extension provides the option to model reciprocal interactions between browsing populations and landscape distributions of available forage. A conceptual model of the Browse Disturbance extension is outlined in Figures 1 and 2.

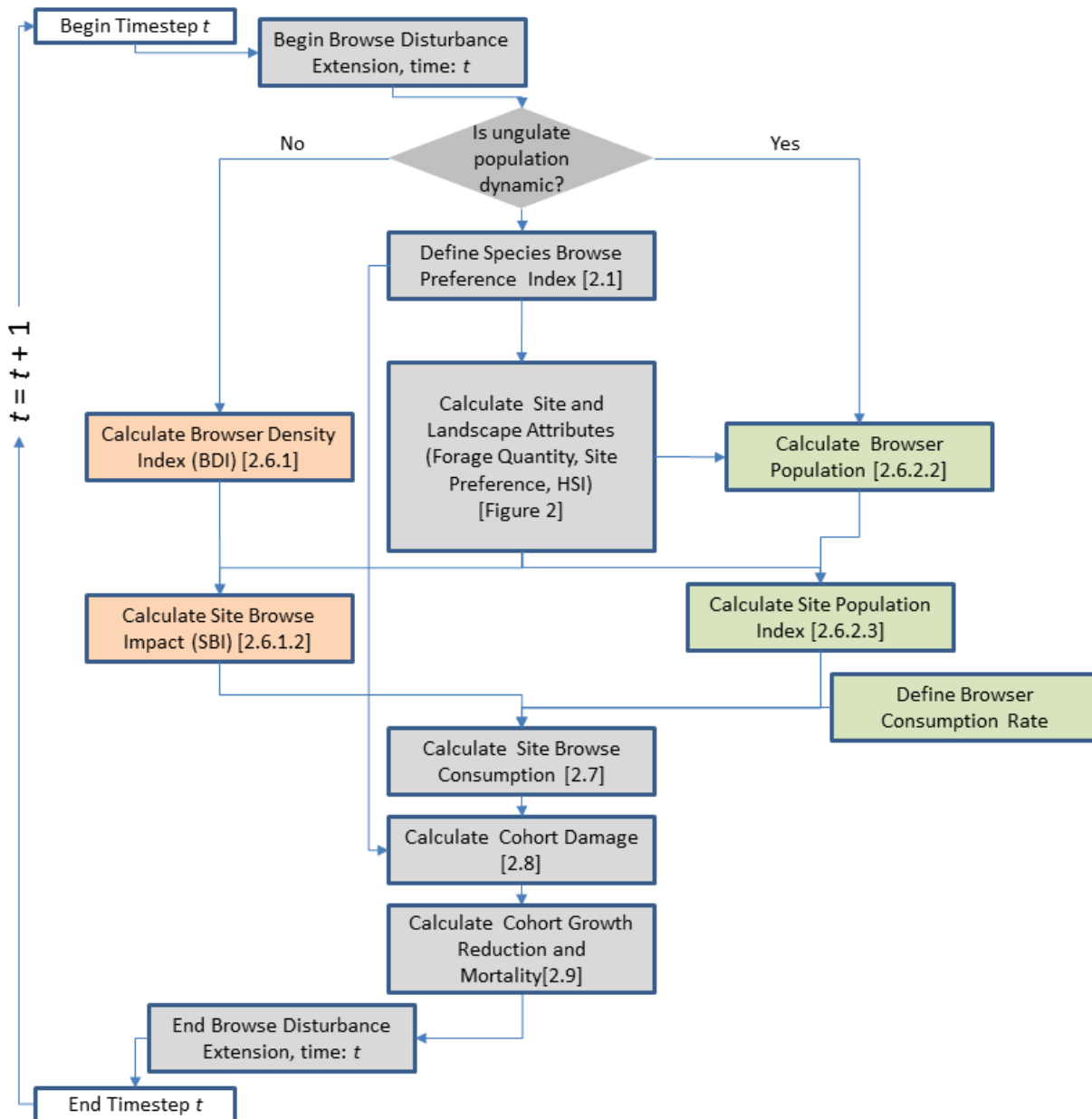


Figure 1. Overall conceptual diagram of Browse Extension.

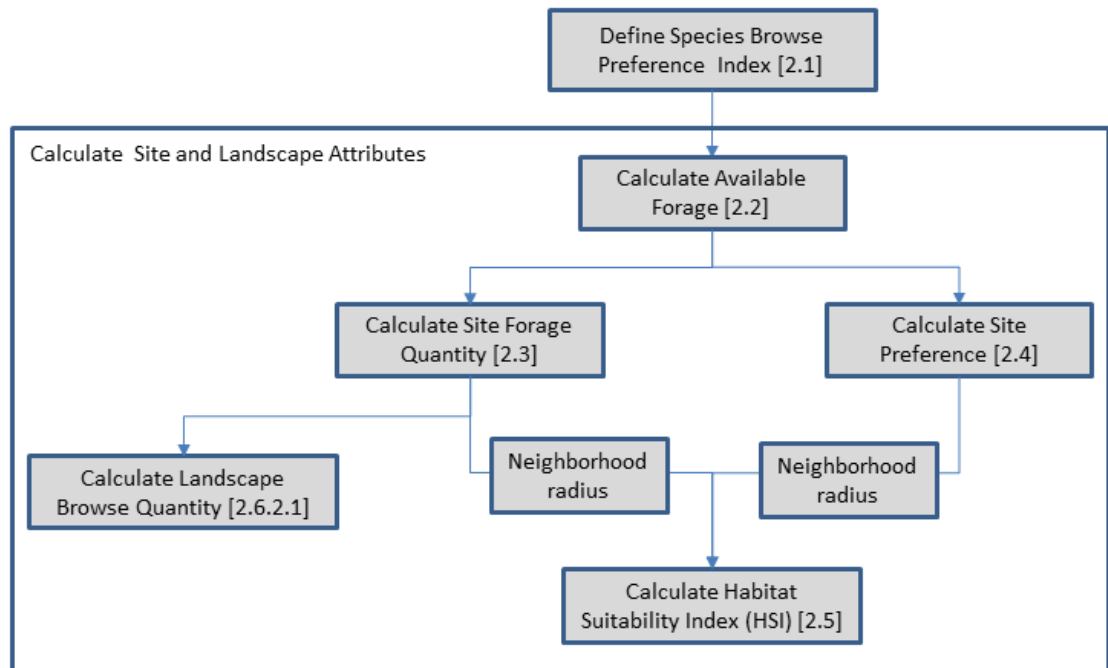


Figure 2. Inset conceptual diagram for calculation of site and landscape attributes.

3 Model Description

3.1 Species Browse Preference Index

Most browsers prefer certain plant species over others. The user must provide a relative preference index for each species. An example of tables bearing categorical values for browse preference by deer in Pennsylvania is provided in addendum 1. Species browse preference is a unit-less index (0-1) that defines the relative selectivity of the browser for certain species. Species with higher values are more preferred than species with lower values. Species with a browse preference of 0 are considered non-forage and therefore do not contribute toward estimates of forage quantity. However, users may include species with browse preference of 0 in calculations of site preference (section 3.5) if they suspect that the presence of non-forage species may influence the palatability of preferred species within the same site. Preference index values should be representative of annual browse preference, taking into account seasonal variability. The relative preference index also is used to determine the proportion of the total available browse biomass that is removed from each species cohort.

3.2 Forage Availability

In nature, the accessibility of biomass to browsers is primarily a function of the height of the biomass above the ground. LANDIS-II does not track the height of cohorts, but because an assumption of LANDIS-II is that sites are fully stocked, the Browse extension uses cohort biomass as a surrogate for height. User-specified parameters are used to define two thresholds used to calculate forage availability. The first threshold specifies an amount of cohort biomass below which the entire cohort is available as forage and above which a portion of the cohort biomass can “escape” browsing because it is assumed that that biomass is above the reach of the herbivores. The second threshold is the amount of biomass above which the entire cohort has “escaped” the reach of the herbivores and is not available as forage biomass. Actual biomass available as forage is calculated according to the fraction of annual growth that susceptible cohorts allocate to leaf and stem material (**section reference here**).

3.2.1 Susceptible Cohorts

The `MinEscapeThreshold` parameter specifies the first threshold, which is the proportion of the maximum possible-site biomass (calculated by the succession extension) below which cohorts having less than that biomass cannot escape browsing. For example, if site has a maximum possible biomass of 10000 g/m², then a `MinEscapeThreshold` value of 0.05 means that cohorts with biomass ≤ 500 g/m² are fully available as forage. As site biomass exceeds this threshold, the `MaxEscapeThreshold` parameter specifies how high a cohort’s biomass must be to fully “escape” herbivory. To continue the example, if site has a maximum possible biomass of 10,000 g/m², then a `MinEscapeThreshold` value of 0.1 means that cohorts with biomass ≥ 1000 g/m² have escaped herbivory and none of their biomass would be available as forage.

Because sites often contain a mixture of species and cohort sizes, these calculations are not made by individual cohorts, but for all cohorts taken together. In some cases (only small cohorts are on the site), all cohorts may be

susceptible, in other cases parts of cohorts may be susceptible, and in others (e.g., only large cohorts on the site), no cohorts may be susceptible. Starting with the cohort with the lowest biomass (regardless of species preference and age), the proportion of the cohort available as forage is computed as $1 - (\text{cohort biomass} - \text{minimum biomass threshold})$, with a minimum of 0.0, and the computed biomass available as forage is added to an available forage pool. If the size of the pool is less than the biomass threshold computed from the `MinEscapeThreshold`, the next cohort in order of increasing biomass is then considered. The difference between the size of the pool and the original biomass threshold is used as a new threshold for the second cohort. This sequence is iterated for cohorts until the size of the pool is equal to the original biomass threshold, or until all cohorts have been considered. Once the available forage pool has reached the minimum biomass threshold, increasingly large cohorts are processed in a similar way, except that the proportion of biomass available as forage decreases linearly as the available forage pool approaches the maximum biomass threshold computed using `MaxEscapeThreshold`. This assumes that apical dominance within low-statured cohorts will cause the browsing of lower branches to be compensated by growth beyond the browse line (McLaren and Peterson 1994, Vila et al. 2002), allowing cohorts to gradually escape herbivory. Here the proportion of the cohort available as forage is computed as $1 - (\text{cohort biomass} - \text{maximum biomass threshold})$, with a minimum of 0.0, and the computed biomass available as forage is added to an available forage pool. This process is iterated until the size of the available forage pool is equal to the maximum biomass threshold, or until all cohorts have been considered.).

Note that an age threshold as a proportion of longevity is used to prevent senescing mature cohorts from being treated as cohorts within browse reach. Cohorts with ages greater than this age threshold (default is 57% of longevity; see 4.2.10) are not considered as eligible for forage.

3.2.2 Available forage biomass

Available forage biomass is calculated as the annual growth allocated to stems and twigs. Browsing herbivores typically remove leaf material from deciduous trees during summer and remove stem material from deciduous trees during winter. They also tend to avoid browsing conifers during the summer, but remove both stems and the needles attached to them in winter (Persson et al. 2000). Hence, both new leaf and twig material are annually available to foraging herbivores. By default, the extension assumes that 33% of annual growth is allocated to leaves and 33% is allocated to twigs, for a total of 66% of annual growth that is available as forage biomass. This assumption is based on general allocation patterns observed across a wide range of tree species with different life history attributes (Niklas and Enquist 2002). The user can supply a different proportion of ANPP (4.2.7). Users can also apply an option to count 100% of new growth as browseable material during the first year of growth (cohort age = 1).

3.3 Population Zones

Spatial heterogeneity in browsing pressure caused by heterogeneity in either relative or absolute ungulate densities (see Section 2.6 below) can optionally be defined as different population zones within the Browse Disturbance extension.

The user may specify spatial zones (termed Population Zones) that represent different regions of the simulated landscape with independent population densities. These zones are defined as an input raster map with map values corresponding to the different Population Zones. If no zone map is provided, the entire simulation area is treated as a single zone.

3.4 Site Forage Quantity

Site forage quantity is an output raster map of the total amount of available forage (g/m^2) on each site (cell in the raster). Available forage (as defined in 3.2) is summed for all species-cohorts present on each site. Cohorts with species preference values (as defined in 3.1) of 0 are considered non-forage, and are not included in the calculation of site forage quantity.

3.4.1 Zone Forage Quantity

The total forage quantity for each population zone (Z , see 3.3) is summed from the site forage quantity values.

$$ForageQuantity_Z = \sum ForageQuantity_{site}$$

Zone forage quantity is used in the calculation of zone carrying capacity (when using the Dynamic Browser Population [2.6.2]) and to rescale the site forage quantity (2.4.2)

3.4.2 Rescaled Forage Quantity

A rescaled site forage quantity value is calculated so that the sum of the rescaled values sums to 1.0 in each zone (Z , see 3.3).

$$Quantity_{rescale}_{site} = \frac{ForageQuantity_{site}}{ForageQuantity_Z}$$

The rescaled site quantity is used calculate site browse impacts (3.7.2) or site population density (3.7.3.3), and serves as a component in downscaling the zone population to the site-scale.

3.5 Site Preference

Site preference is an output raster map of the average preference value for available forage on each site (cell), and is an indicator of forage “quality”. The value is calculated as a weighted average of either:

- A) the preference values for all species-cohorts present in a cell, or
- B) the preference values for species-cohorts with >0 preference,

where the weighting is based on the cohorts’ available forage (as defined in 3.2). Users should choose option A if they suspect that the presence of non-forage species at a site could reduce the susceptibility of preferred species-cohorts to browsing. The default behavior is option B, but users can choose option A with the optional “CountNonForageSitePref” parameter (4.2.13).

3.6 Habitat Suitability Index

To account for the spatial pattern of available browse and how it might influence whether any one site (cell) is browsed, a Habitat Suitability Index (HSI) raster is

calculated. Users have the option to calculate the HSI using a moving window of a specific size if they assume that the quantity and/or quality of available browse in the surrounding neighborhood of sites will impact the susceptibility of sites to browsing. Options for calculating HSI include:

- A) neighborhood average of site forage quantity (3.2),
- B) neighborhood average of site preference (3.5),
- C) the product of A and B.

If the user does not choose to implement the moving window algorithm (neighborhood radius = 0), then HSI will be based on site-specific A, B or C.

3.6.1 2.6.1 Rescaled HSI

A rescaled HSI value is calculated so that the sum of the rescaled values sums to 1.0 in each zone (Z , see 2.3).

$$HSI_{rescale_{site}} = HSI_{site} \div \sum HSI_{site}$$

The rescaled HSI values are used as a component a component in downscaling the zone population to the site-scale.

3.7 Browser Population Density

The browse disturbance extension provides users with two alternative options to define browse pressure related to ungulate density. The first (elaborated in Section 3.7.1) implements a user-defined browser density across the landscape or within different spatial zones (defined above). Under this option, the user defines how browser densities vary in time and space as a modeling scenario (i.e., they are pre-determined by the user). This option will be most applicable where browser density is primarily defined by external factors such as hunting activities. The second option (elaborated in Section 3.7.3) explicitly models browser population dynamics as a function of forage availability and user-supplied mortality rates. Regardless of the browser density option used, the user may specify population zones (3.3) that represent different regions of the simulated landscape with independent browser densities. If no zone map is provided, the entire simulation area is treated as a single zone and single population.

3.7.1 Density Option 1: Browser Density Index (BDI)

The Browser Density Index is a user-supplied value between 0 and 1 that represents the population density relative to its capacity for browsing impacts. For example, a BDI value of 0.50 represents a density which would, on average, consume 50% of available forage. A value of 1.0 would be an extreme case where 100% of available forage would be consumed, representing densities at (or above) the carrying capacity. Values are provided by the user for each Population Zone (2.3). When multiple population zones exist within the simulation area the user has the option to ‘smooth’ the distribution of BDI using a moving window average of the BDI values. After smoothing, each site has its own BDI value (BDI_{site}).

3.7.2 Site Browse Impact (SBI)

The site browse impact temporary raster uses the total browse impact for a zone, the rescaled local HSI (2.6.1) values and the rescaled site forage quantity (2.4.2) to estimate local browse impacts, computed as a rate of browse removal for each site. The total browse impact (TBI_Z) for zone (Z) is calculated by summing the BDI values of all sites in the zone.

$$TBI_Z = \sum BDI_{site}$$

As the browse density index (BDI) approaches 1.0, the HSI value has less influence on the distribution of site browse impact (SBI). In the extreme case of BDI of 1.0, where all available forage will be consumed, impacts must be distributed in proportion to the quantity of available forage on each site. Therefore, the site browse impact is the product of total zone impact TBI_Z and a weighted average of [HSI_{rescale}] (2.6.1) and [Quantity_{rescale}] (2.4.2), where BDI (2.7.1) provides the weighting.

$$SBI_{site} = TBI_Z \times [(Quantity_{rescale}_{site} \times BDI_{site}) + (HSI_{rescale}_{site} \times (BDI_{site} - 1))]$$

In essence, this is the BDI value downscaled to the site-level using the HSI and forage quantity values. It is possible for this calculation to result in a SBI value greater than one, which would indicate a removal of more than 100% of the available forage. To account for this artifact, SBI values are capped at 1.0, and the remainder beyond 1 is recorded and summed across sites within a zone. The total remainder is then allocated equally (not biased by HSI or forage quantity) to sites with initial SBI values less than 1. This approach will maintain an average SBI value equal to the zone BDI, with a spatial bias determined by HSI values and forage quantity.

3.7.3 Density Option 2: Dynamic Browser Population (DBP)

Ungulate populations are influenced by density-dependent growth and mortality, along with other factors that may reduce population density (e.g. hunting, predation, disease outbreaks). Under the DBP option, density-dependent changes in the ungulate populations are modeled according to the discrete-time quadratic model (May 1975), which models population increases or decreases in relation to a population carrying capacity. When the animal population exceeds its carrying capacity, animal mortality exceeds recruitment and the population declines. When the animal population is less than carrying capacity, recruitment of new animals exceeds mortality and the population increases. The carrying capacity of the animal population is estimated by the annual forage requirements for individual animals in the population in relation to the forage biomass available across the landscape. Additional factors also reduce ungulate populations and are modeled accordingly (e.g. harvest, stochastic mortality, and predation). Stochasticity is incorporated by parameter estimates for population growth and mortality factors using mean estimates and normal distributions.

3.7.3.1 Calculate Zone Carrying Capacity

The carrying capacity of the browser population is defined as the forage quantity available across the landscape in relation to the annual intake rate of the population. The total available forage in the population zone is calculated as the

sum of site forage quantity across all sites in the zone (2.4.1). Zone carrying capacity is determined by dividing the total forage quantity by the annual consumption rate for the browser population, which is supplied by the user.

3.7.3.2 Calculate Browser Population

Changes in the browser population are modeled according to the discrete-time quadratic model (May 1975):

$$\Delta N_{t,Z} = R_Z N_{t,Z} \left(1 - \frac{N_{t,Z}}{K_Z}\right) - \sum M_Z N_{t,Z}$$

Where $\Delta N_{t,Z}$ is the change in browser population density N at time t in Population Zone Z , R_Z is a user-supplied population growth rate for zone Z and $\sum M_Z N_{t,Z}$ is the sum of all reductions in the population due to mortality factors. Users can supply mortality rates for A) generic mortality (any factor that might reduce population density), B) harvesting (population management), and C: predation. K_Z is the carrying capacity for the browser population (2.7.2.1). The estimated population ($\Delta N_{t,Z} + N_{t-1,Z}$) is recorded in the log file as the population, but the effective population (N_{Eff}) is the minimum of the population and K_Z . N_{Eff} is used for all subsequent calculations including browse impacts and population growth the following year.

3.7.3.3 Calculate Site Population Index

The site population index raster combines the zone population (2.7.2.2), the rescaled local HSI (2.6.1) values and the rescaled site forage quantity (2.4.2) to estimate local populations of browsers. This process distributes the zone population to sites as a function of the HSI values and forage quantity in a manner directly analogous to the spatial distribution of BDI to local SBI values (2.7.1.2). Here, the spatial distribution of population is influenced by the population proximity to carrying capacity (K , 2.7.2.1). As a population approaches K , the distribution must more closely match the distribution of available forage and HSI has less influence on population distribution. In the extreme case of the population at (or above) K , then the distribution of the population must be distributed in proportion to the quantity of available forage on each site. Therefore, the site population (Pop_{site}) is the product of total zone population (Pop_Z) and a weighted average of [HSIrescale] (2.6.1) and [Quantity_rescale] (2.4.2), where the ratio of Pop_Z to K provides the weighting.

$$Pop_{site} = Pop_Z \times \left[\left(Quantity_resacle_{site} \times \frac{Pop_Z}{K} \right) + \left(HSIresacle_{site} \times \left(\frac{Pop_Z}{K} - 1 \right) \right) \right]$$

3.8 Site Browse Consumption

If using defined browser densities (2.6.1), the SBI (2.6.1.3) determines the overall browse rate for a site. The total amount of forage to be removed on a site is the product of the SBI and the Site Forage Quantity (2.3). If using the dynamic browser densities (2.6.2), the defined browser consumption rate is multiplied by the site population index (2.6.2.3) to calculate the total amount of forage to be removed.

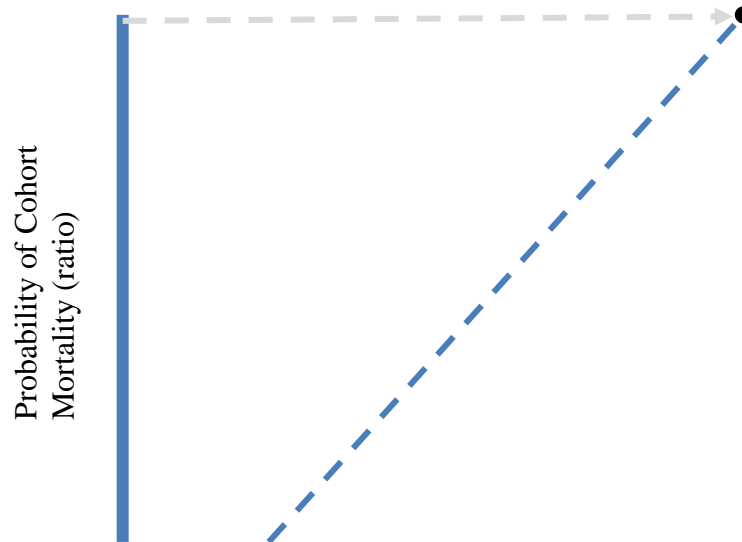
3.9 Cohort Damage

Within a site, biomass is removed from cohorts (i.e., they are damaged) preferentially according to species preferences. The total amount of forage to be removed from a site is first calculated (2.7). Then, species-cohorts are rank-ordered by their preference values (2.1). These values not only rank species, but define a target removal percentage (i.e., a 0.8 preference equates to 80% consumption of that species). Forage biomass is first removed from species with the highest browse preference (all species with the same rank are treated equivalently), up to the target removal rate for the species-cohort. If more biomass needs to be removed to reach the calculated total amount of forage for the site, then biomass is removed from the next most preferred species-cohort, again up to the species-cohort's target removal rate. This procedure is iterated for all species until the biomass to be removed is satisfied, or all cohorts have been browsed at their target removal rates. If browse removal using the defined target removal rates does not meet the required total amount of forage, then additional biomass is removed again starting with the most preferred species. The biomass removal needed to meet the target is removed from the most preferred species until all available biomass has been removed from that species (i.e., now ignoring the target removal rate for the species). Any remaining biomass to be removed comes from the next most preferred species, and continues down the preference list until either the demand for removed biomass is met, or all available biomass is removed from the site.

Example: A site has a SBI of 0.45 and 100 g/m² available forage, translating to a total forage removal of 45 g/m². There are 2 cohorts on the site, one high preference (0.85) and one low preference (0.165). If the high preference cohort has 30 g/m² available forage, which gets browsed at a rate equal to its species preference (0.835), then 25 g/m² is removed from this cohort. The second cohort is low preference with 70 g/m² available forage. This cohort will be browsed at its removal rate (0.165) to have 12 g/m² forage removed. The total forage consumed (37 g/m²) is less than the total target removal for the site (45 g/m²). The remaining forage to be removed (8 g/m²) comes from the most preferred species first, up to its total available forage. In this case, an additional 5 g/m² can be removed from the highly preferred cohort for a total removal of all 30 g/m². The remaining 3 g/m² is removed from the less preferred cohort for a total of 15 g/m².

3.10 Browse Effect on Cohort Growth and Mortality

The browse disturbance extension also models the effects of biomass removal on subsequent cohort growth and survival via separate user-defined threshold proportions of annual growth lost (see Figure 3). Browse rates above these thresholds (a) lead to growth reduction (losses) in the following year, and/or increased probability of mortality prior to the following year. When browse rates



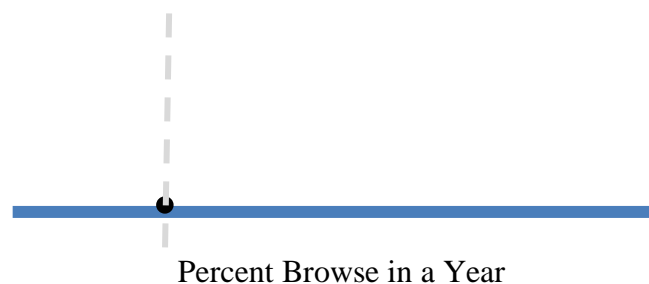
are above the minimum threshold (a, Figure 3), growth losses and mortality increase linearly to maximums (b, Figure 3) set by the user.

Figure 3. Effects of browse on cohort mortality and growth reduction. A user-defined threshold (a) determines the minimum amount of browse for any effect, and a second user-defined threshold (b) determines the maximum effect when browse is 100%.

Areas for additional development

Stochasticity –where and how.

Seed predation



3.11 Literature Cited

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4 Input Files

4.1 Input File Rules

The input rules for the Dynamic Browse Extension are identical to those of the LANDIS-II Core Model. Please see the LANDIS-II Core User's Guide for further instruction.

4.2 Input File Parameters

4.2.1 Extension title, time step

The first parameter is the title of the input file:

```
LandisData "Dynamic Ungulate Browse"
```

The second parameter is the time step in years, which should always be 1. For example:

```
Timestep      1
```

4.2.2 Species Inputs

The keyword "SpeciesTable" denotes the section of the input file for providing species-specific parameters. The table consists of 6 columns of values, with each row corresponding to a tree species. All species do not have to be listed and they may appear in any order. If a species is listed, all 6 parameter values must be provided.

4.2.2.1 *Species Name*

The first column in the SpeciesTable is the species name. The names must match the species names in the simulation's main species input file.

4.2.2.2 *Preference*

The second column in the SpeciesTable is the species preference. This value must range between 0 and 1, and represents the relative rate of consumption of the browser for this species. Species with a preference of 0 are not considered forage for the browser, and will never be damaged by the browser. Any species not listed in the SpeciesTable will have a default preference of 0.

4.2.2.3 *Growth Reduction Threshold*

The third column in the SpeciesTable is the threshold of proportion browsed at which growth reduction begins (a in Figure 3). Threshold values should generally range between 0 and 1, but values outside this range are acceptable to achieve > 0 growth reduction at very low browse proportions. In all cases, 0% browsed results in no growth reduction.

4.2.2.4 *Growth Reduction Maximum*

The fourth column in the SpeciesTable is the maximum growth reduction caused by 100% browse (b in Figure 3). Threshold values should generally range between 0 and 1, but values outside this range are acceptable to achieve 100% growth reduction at a proportion browsed <1 . In all cases, growth reduction is capped at 100%.

4.2.2.5 *Mortality Threshold*

The fifth column in the SpeciesTable is the threshold of proportion browsed at which cohort mortality begins (a in Figure 3). Threshold values should generally range between 0 and 1, but values outside this range are acceptable to achieve >0 mortality probability at very low browse proportions. In all cases, 0% browse results in no mortality.

4.2.2.6 *Mortality Maximum*

The sixth column in the SpeciesTable is the maximum mortality probability caused by 100% browse (b in Figure 3). Threshold values should generally range between 0 and 1, but values outside this range are acceptable to achieve 100% mortality at a browse proportion <1 . In all cases, mortality is capped at 100%.

4.2.2.7 *Biomass Maximum*

The sixth column in the SpeciesTable is the maximum biomass attainable by each species (in g m^{-2}). This value should match the maximum biomass used for the chosen succession extension (Biomass Succession or NECN Succession). Biomass Maximum no longer varies at the ecoregion level; rather, it is constant for each species across the entire landscape.

4.2.3 Zone Map

The keyword “ZoneMap” is followed by a raster map file name that defines the population zones within the landscape (3.3).

4.2.4 Population File

The keyword “PopulationFile” is followed by a file name pointing to a text input file that defines the initial populations/browser density index for each zone.

4.2.5 Dynamic Population File (Optional)

The keyword “DynamicPopulationFile” is followed by a file name pointing to a text input file that defines the additional population parameters required when modeling a dynamic population (3.7.3). This parameter should be excluded when using defined populations (3.7.1). The presence of this parameter and associated file trigger the extension to model dynamic populations and to treat the values in the PopulationFile (4.2.4) as initial populations instead of browser density indices.

4.2.6 Consumption Rate

The keyword “ConsumptionRate” is followed by an integer value representing the annual forage requirements (kg) for an individual browser.

4.2.7 ANPP Forage Proportion

The keyword “ANPPForageProp” is followed by a decimal value between 0 and 1 representing the proportion of annual growth that is assumed to be available as forage. The default value for this parameter is 0.66 (see 3.2.2).

4.2.8 Minimum Browse in Reach Proportion

The keyword “MinBrowsePropinReach” is followed by a decimal value between 0 and 1 representing the minimum proportion of a cohort’s available forage that must be considered within browser reach in order for the cohort to be susceptible to browsing (3.2.1). Cohorts with browse in reach proportions less than this threshold are considered “escaped” from the browse reach, and none of their forage is available to the browser.

4.2.9 Browse Biomass Threshold

The keyword “BrowseBiomassThreshold” is followed by a decimal value between 0 and 1 representing the proportion of the ecoregion maximum potential biomass when a cohort begins to escape browse (3.2.1). This proportion (multiplied by the ecoregion maximum potential biomass) defines the threshold at which cumulative biomass represents cohorts above the reach of browsers.

4.2.10 Proportion of Longevity to Escape Browse

The keyword “EscapeBrowsePropLong” is followed by a decimal value between 0 and 1 representing the proportion of longevity at which cohorts are considered to have escaped from browse (3.2.1). This age threshold is used to prevent senescing mature cohorts from being treated as cohorts within browse reach as their biomass declines.

4.2.11 Growth Reduction Option (Optional)

The keyword “GrowthReduction” is followed by “ON” or “OFF” to turn the browse impacts on the following year’s growth on or off (3.10). This is an optional parameter. The default is “ON”, and excluding this parameter will include simulation of growth reductions.

4.2.12 Mortality Option (Optional)

The keyword “Mortality” is followed by “ON” or “OFF” to turn the browse impacts on cohort mortality on or off (3.10). This is an optional

parameter. The default is “ON”, and excluding this parameter will include simulation of cohort mortality.

4.2.13 Count Non-Forage in Site Preference Option (Optional)

The keyword “CountNonForageinSitePref” is followed by “TRUE” or “FALSE” to set whether cohorts with preference values of 0 should be used in the calculation of average site preference (3.5). This is an optional parameter. The default is “FALSE”, and excluding this parameter will follow option B as described in 3.5.

4.2.14 Use Initial Biomass as Forage Option (Optional)

The keyword “UseInitBiomassAsForage” is followed by “TRUE” or “FALSE” to set whether the forage of new cohorts (age = 1) includes all of the initial biomass. This is an optional parameter. The default is “FALSE”, and excluding this parameter will apply the ANPPForageProp (4.2.7) to the initial biomass when determining the forage of a new cohort.

4.2.15 HSI Inputs

The HSI inputs list the components (ForageQuantity and/or SitePreference) that should be included in the HSI calculation along with any neighborhood window that should be used for each component. The HSI Inputs table can include one or two rows depending on the user’s choice of HSI components (3.6). If both ForageQuantity and SitePreference are included, ForageQuantity should be listed first, and the resulting HSI is the product of the forage quantity and site preference values.

4.2.15.1 *Forage Quantity (Optional)*

The keyword “ForageQuantity” is followed by a positive integer value defining a neighborhood radius. When the radius is >0 , then the site forage quantity used in the HSI calculation is the average forage quantity of all sites within the defined neighborhood. If this parameter is excluded, forage quantity will not be used to calculate HSI. Either ForageQuantity or SitePreference (or both) must be listed in the HSI Inputs.

4.2.15.2 *Site Preference (Optional)*

The keyword “SitePreference” is followed by a positive integer value defining a neighborhood radius. When the radius is >0 , then the site preference used in the HSI calculation is the average site preference of all sites within the defined neighborhood. If this parameter is excluded, site preference will not be used to calculate HSI. Either ForageQuantity or SitePreference (or both) must be listed in the HSI Inputs.

4.2.16 Output Maps (Optional)

Five potential output maps have been defined for this extension. The generation of any of the output maps can be turned on or off by including or excluding it from the parameter file.

4.2.16.1 *Site Preference Output Maps (Optional)*

The keyword “SitePrefMapNames” is followed by a path and filename template for output maps of site preference (3.5). The filename should include the key “{timestep}” to indicate where the value of the timestep should be included in the file name. This output map is optional.

4.2.16.2 *Site Forage Output Maps (Optional)*

The keyword “SiteForageMapNames” is followed by a path and filename template for output maps of site forage quantity (3.4). The filename should include the key “{timestep}” to indicate where the value of the timestep should be included in the file name. This output map is optional.

4.2.16.3 *Site HSI Output Maps (Optional)*

The keyword “SiteHSIMapNames” is followed by a path and filename template for output maps of site habitat suitability (3.6). The filename should include the key “{timestep}” to indicate where the value of the timestep should be included in the file name. This output map is optional.

4.2.16.4 *Site Population Output Maps (Optional)*

The keyword “SitePopulationMapNames” is followed by a path and filename template for output maps of site population (3.7.2, 3.7.3.3). The filename should include the key “{timestep}” to indicate where the value of the timestep should be included in the file name. This output map is optional.

4.2.16.5 *Biomass Removed Output Maps (Optional)*

The keyword “BiomassRemovedMapNames” is followed by a path and filename template for output maps of biomass removed. The filename should include the key “{timestep}” to indicate where the value of the timestep should be included in the file name. This output map is optional. Biomass removed includes biomass consumed by the browser (3.8) as well as biomass lost to mortality caused by browsing (3.10).

4.2.17 Output Log

The keyword “LogFile” is followed by a path and filename for the output log to be written.

5 Output Files

5.1 Site Preference Output Maps (Optional)

The inclusion of “SitePrefMapNames” in the parameter file generates output maps of Site Preference values. Map values are site preference values multiplied by 100, for a range of 0 to 100. Non-active cells always have a site preference of 0.

5.2 Site Forage Output Maps (Optional)

The inclusion of “SiteForageMapNames” in the parameter file generates output maps of site Forage Quantity values. Map values are forage quantity in g/m². Non-active cells always have a forage quantity of 0.

5.3 Site HSI Output Maps (Optional)

The inclusion of “SiteHSIMapNames” in the parameter file generates output maps of site Habitat Suitability Index values. Map values depend on the components (site preference and/or forage quantity) used in the HSI calculation. Non-active cells always have HSI values of 0.

5.4 Site Population Output Maps (Optional)

The inclusion of “SitePopulationMapNames” in the parameter file generates output maps of site population. Map values depend on whether the option of dynamic populations was used. With non-dynamic populations, the map values represent the Site Browse Index (3.7.2) value multiplied by 100, for a range of 0 to 100. With dynamic populations, the map values represent the Site Population Index (3.7.3.3). Non-active cells always have population values of 0.

5.5 Biomass Removed Output Maps (Optional)

The inclusion of “BiomassRemovedMapNames” in the parameter file generates output maps of site biomass removed values. Map values are biomass in g/m². Biomass removed includes biomass consumed by the browser (3.8) as well as biomass lost to mortality caused by browsing (3.10). Non-active cells always have a biomass removed of 0.

5.6 Output Log

The output log is a text file that contains information about the browse events over the course of a simulation. For each timestep, the log includes separate records for each population zone (3.3) and for the landscape as a whole.

5.6.1 Timestep

The simulation timestep.

5.6.2 Zone

The population zone map code. Records representing the full landscape have a Zone value of -1.

5.6.3 Population

The total zone/landscape population (dynamic population) or browser density index (non-dynamic population). Units: # of individuals.

5.6.4 Total Forage (kg)

The total zone/landscape forage quantity. Units: kg biomass.

5.6.5 Carrying Capacity (K)

The maximum number of browsers that could be supported in the zone/landscape based on the total forage available. Units: # of individuals.

5.6.6 Effective Population

The minimum of Population and K, used in subsequent browse impact calculations. Units: # of individuals.

5.6.7 Damaged Sites

Number of sites in the zone/landscape damaged by the browser.

5.6.8 Biomass Removed (g/m^2)

Total biomass removed from the zone/landscape by the browser due to direct browsing. Units: g/m^2 .

5.6.9 Biomass Mortality (g/m^2)

Total biomass removed from the zone/landscape by the browser due to browse-induced mortality. Units: g/m^2 .

5.6.10 Cohorts Killed

Number of cohorts killed in the zone/landscape by the browser. Units: # of cohorts.

5.6.11 Biomass Removed by species

Total species biomass removed from the zone/landscape by the browser due to direct browsing and mortality. A column is included for each species. Units: g/m^2 .

5.6.12 Cohorts Killed by species

Total number of cohorts killed for each species within the zone/landscape by the browser. A column is included for each species.

6 Example Input Files

6.1 Dynamic Ungulate Browse

```
LandisData  "Dynamic Ungulate Browse"
```

```
Timestep 1
```

```
<< Species Inputs >>
```

```
SpeciesTable
```

```
>>                                     -GrowthReduction-  ---Mortality---
>> Name          Preference  Threshold  Max  Threshold  Max
>> -----
    abiebals      0.0        0.5        0.4  0.5        0.1
    acerrubr      0.3        0.5        0.4  0.5        0.1
    acersacc      0.5        0.5        0.4  0.5        0.1
    betualle      0.3        0.5        0.4  0.5        0.1
    betupapy      0.6        0.5        0.4  0.5        0.1
    fraxamer      0.6        0.5        0.4  0.5        0.1
    piceglau      0.0        0.5        0.4  0.5        0.1
    pinubank      0.0        0.5        0.4  0.5        0.1
    pinuresi      0.0        0.5        0.4  0.5        0.1
    pinustro      0.0        0.5        0.4  0.5        0.1
    poputrem      0.4        0.5        0.4  0.5        0.1
    querelli      0.0        0.5        0.4  0.5        0.1
    querrubr      0.0        0.5        0.4  0.5        0.1
    thujocci      0.5        0.5        0.4  0.5        0.1
    tiliamer      0.4        0.5        0.4  0.5        0.1
    tsugcana      0.5        0.5        0.4  0.5        0.1
```

```
<< Browser population Inputs >>
```

```
ZoneMap  ecoregions.gis
```

```
PopulationFile  DefinedUngulatePopulation.txt
```

```
DynamicPopulationFile  DynamicUngulatePopulation.txt  <<Optional
```

```
ConsumptionRate  745  << kg/yr/individual
```

```
<< Forage Inputs >>
```

```
ANPPForageProp      0.66  <<Prop of ANPP that counts as forage
```

MinBrowsePropinReach 0.50 <<Min prop of browse within reach for a cohort to be browsed

BrowseBiomassThreshold 0.05 <<Proportion of ecoregion max biomass when cohort begins to escape browse

EscapeBrowsePropLong 0.57 <<Prop of longevity when browse is escaped

<< Options >>

<<GrowthReduction OFF << Default is ON

<<Mortality OFF << Default is ON

<<CountNonForageinSitePref TRUE << Default is FALSE

<<UseInitBiomassAsForage TRUE << Default is FALSE

<< HSI Inputs >>

<< Component Neighborhood >>

<< -----

<<ForageQuantity 0 << ForageQuantity and/or SitePreference

SitePreference 500 << ForageQuantity and/or SitePreference

<< Output Maps >>

SitePrefMapNames browse/SitePref_{timestep}.gis

SiteForageMapNames browse/SiteForage_{timestep}.gis

SiteHSIMapNames browse/HSI_{timestep}.gis

SitePopulationMapNames browse/Pop_{timestep}.gis

BiomassRemovedMapNames browse/BioRemoved_{timestep}.gis

<< Output Logs >>

LogFile browse/browse_log.csv

6.2 Defined Ungulate Population

LandisData "Defined Ungulate Population"

>>Year Zone Browser Density Index

>>-----

0 1 0.5

0 2 0

6.3 Dynamic Ungulate Population

LandisData "Dynamic Ungulate Population"

R

<<Min	Max
-------	-----

<<---	---
-------	-----

0.3	0.4
-----	-----

Mortality

<<Min	Max
-------	-----

<<---	---
-------	-----

0.0	0.0
-----	-----

Predation

<<Min	Max
-------	-----

<<---	---
-------	-----

0.0	0.0
-----	-----

Harvest

<<Min	Max
-------	-----

<<---	---
-------	-----

0.0	0.0
-----	-----

7 Addendum 1

Tables containing categorical values of browse preference for forest species in Pennsylvania are from Table 4 of the Latham et al. (2005) report.

tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
<i>Abies balsamea</i>	balsam fir		
<i>Acer negundo</i>	boxelder	not preferred	not preferred
<i>Acer nigrum</i>	black maple	low/moderate	high
<i>Acer pensylvanicum</i>	striped maple	low	low
<i>Acer rubrum</i>	red maple*	low/moderate	high
<i>Acer saccharinum</i>	silver maple	low/moderate	moderate
<i>Acer saccharum</i>	sugar maple*	low/moderate	moderate
<i>Aesculus flava</i>	yellow buckeye	(unknown, but toxic to cattle)	(unknown, but toxic to cattle)
<i>Aesculus glabra</i>	Ohio buckeye	(unknown, but toxic to cattle)	(unknown, but toxic to cattle)
<i>Amelanchier arborea</i>	downy serviceberry	(is browsed)	(is browsed)
<i>Amelanchier laevis</i>	Allegheny serviceberry	(is browsed)	(is browsed)
<i>Aralia spinosa</i>	devils-walkingstick	not preferred	not preferred
<i>Asimina triloba</i>	pawpaw	not preferred	not preferred
<i>Betula alleghaniensis</i>	yellow birch*	low/moderate	high (late autumn)
<i>Betula lenta</i>	sweet birch*	low/moderate	high (late fall)
<i>Betula nigra</i>	river birch	low	moderate

tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
<i>Betula papyrifera</i>	paper birch	low/moderate	high (late fall)
<i>Betula populifolia</i>	gray birch	low/moderate	moderate
<i>Carpinus caroliniana</i>	American hornbeam		
<i>Carya cordiformis</i>	bitternut hickory*	low	low
<i>Carya glabra</i>	pignut hickory	low	low
<i>Carya laciniosa</i>	shellbark hickory	low	low
<i>Carya ovalis</i>	sweet pignut hickory (red hickory)	low	low
<i>Carya ovata</i>	shagbark hickory*	low	low
<i>Carya tomentosa</i>	mockernut hickory*	low	low
<i>Castanea dentata</i>	American chestnut		
<i>Castanea pumila</i>	Allegheny chinkapin		
<i>Celtis occidentalis</i>	hackberry	low	low
<i>Celtis tenuifolia</i>	Georgia hackberry (dwarf hackberry)	low	low
<i>Cercis canadensis</i>	eastern redbud		
<i>Chamaecyparis thyoides</i>	Atlantic white-cedar	low	moderate
<i>Chionanthus virginicus</i>	fringetree	low	low
<i>Cornus alternifolia</i>	alternate-leaf dogwood	moderate	high
<i>Cornus florida</i>	flowering dogwood	moderate	high
<i>Crataegus brainerdii</i>	Brainerd hawthorn	low	high
<i>Crataegus calpodendron</i>	pear hawthorn	low	high
<i>Crataegus coccinea</i>	scarlet hawthorn	low	high
<i>Crataegus crus-galli</i>	cockspur hawthorn	low	high

tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
<i>Crataegus dilatata</i>	broadleaf hawthorn	low	high
<i>Crataegus flabellata</i>	fanleaf hawthorn	low	high
<i>Crataegus intricata</i>	Biltmore hawthorn	low	high
<i>Crataegus mollis</i>	downy hawthorn	low	high
<i>Crataegus pruinosa</i>	frosted hawthorn	low	high
<i>Crataegus punctata</i>	dotted hawthorn	low	high
<i>Crataegus rotundifolia</i>	fireberry hawthorn	low	high
<i>Crataegus succulenta</i>	fleshy hawthorn	low	high
<i>Diospyros virginiana</i>	common persimmon		
<i>Fagus grandifolia</i>	American beech	low	high
<i>Fraxinus americana</i>	white ash*	low/moderate	high
<i>Fraxinus nigra</i>	black ash	low/moderate	high
<i>Fraxinus pennsylvanica</i>	green ash	low/moderate	high
<i>Fraxinus profunda</i>	pumpkin ash	not preferred	not preferred
<i>Gleditsia triacanthos</i>	honeylocust	(is browsed)	(is browsed)
<i>Gymnocladus dioica</i>	Kentucky coffeetree		
<i>Ilex opaca</i>	American holly	low	low
<i>Juglans cinerea</i>	butternut		
<i>Juglans nigra</i>	black walnut	(is browsed)	(is browsed)
tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
<i>Magnolia acuminata</i>	cucumbertree	low	moderate
<i>Magnolia tripetala</i>	umbrella magnolia	low	low
<i>Magnolia virginiana</i>	sweetbay		
<i>Malus coronaria</i>	sweet crab apple		
<i>Morus rubra</i>	red mulberry		
<i>Nyssa sylvatica</i>	blackgum (black tupelo)*	high	high
<i>Ostrya virginiana</i>	eastern hophornbeam	low	low
<i>Oxydendrum</i>	sourwood		

tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
<i>Prunus angustifolia</i>	Chickasaw plum		
<i>Prunus pensylvanica</i>	pin cherry	high	high
<i>Prunus serotina</i>	black cherry*	low	low
<i>Prunus virginiana</i>	common chokecherry		
<i>Quercus alba</i>	white oak*	moderate	high
<i>Quercus bicolor</i>	swamp white oak	moderate	high
<i>Quercus coccinea</i>	scarlet oak*	moderate	high
<i>Quercus falcata</i>	southern red oak	moderate	high
<i>Quercus imbricaria</i>	shingle oak	moderate	high
<i>Quercus macrocarpa</i>	bur oak	moderate	high
<i>Quercus marilandica</i>	blackjack oak	moderate	high
<i>Quercus montana</i>	chestnut oak*	moderate	high
<i>Quercus muhlenbergii</i>	chinkapin oak (yellow oak)	moderate	high
<i>Quercus palustris</i>	pin oak	moderate	high
<i>Quercus phellos</i>	willow oak	moderate	high
<i>Quercus rubra</i>	northern red oak*	moderate	high

tree species	common name	browsing preference (spring/summer)	browsing preference (fall/winter)
<i>Sorbus decora</i>	showy mountain-ash		
<i>Tilia americana</i>	American basswood*	(is browsed)	(is browsed)
<i>Toxicodendron vernix</i>	poison-sumac		
<i>Tsuga canadensis</i>	eastern hemlock	low	high
<i>Ulmus americana</i>	American elm	(is browsed)	(is browsed)
<i>Ulmus rubra</i>	slippery elm	(is browsed)	(is browsed)
<i>Viburnum prunifolium</i>	blackhaw	moderate	high