

Calibrating SORTIE's recruitment subroutine for southeastern Québec:
Verifying the consistency of parameters

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ABSTRACT

Calibrating SORTIE's recruitment subroutine for southeastern Québec:
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In recent years foresters have used inverse modelling as a tool to predict stand dynamics for use in research and management. Several models predicting recruitment density by species have been developed. There has, however, never been a serious attempt to see if the parameter values for a recruitment model are more or less constant from one site to another. I compared the performance of two dispersal functions (Weibull and lognormal) that can be used in the recruitment subroutine of SORTIE to determine which resulted in higher likelihoods, as well as whether there was a tendency toward species-specific parameter values among sites. Specifically, I calibrated the model for seven species in the deciduous forest of southern Québec at four sites located within 200km of each other. My results support the findings of Greene *et al.*, 2004, that the lognormal function is a better predictor of recruitment than the Weibull function. I also show that the previously suggested value for the parameter converting tree diameter into recruit production is hardly ideal for all species or for a single species across sites. Further, I show that while the estimated mean dispersal distances tended to be species-specific, they were not significantly so as they were swamped by inter-site differences within species. Indeed, it is not at all clear that inverse modelling permits us to characterize the species-specific dispersal parameters for any tree species.

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A BRIEF REVIEW OF THE REGENERATION DYNAMICS OF MID-LATITUDE TREES

Ultimately, any model of plant recruitment by seed requires terms for (1) seed production, (2) seed dispersal, and (3) juvenile survivorship as mediated by seedbed quality and granivores. In this introductory chapter I will focus on these three factors in turn. Although occasionally I will mention herbs or shrubs, generally I will restrict myself to trees. Also, I will ignore asexual reproduction. In particular, I will discuss the limited realism of the SORTIE recruitment subroutine (the one I will be using) in relation to each of these processes. Finally, I will conclude with a discussion of selection logging, and then a brief reminder of why modelling, despite all its pitfalls, is a useful tool for management.

Seed Production

As noted by Harper *et al.* (1970), there is a trade-off for plants: those that produce large seeds will produce fewer of them. This is because seed production is generally considered a costly exercise for plants that typically results in reduced vegetative vigour after a high-magnitude seed production year (Harper, 1977). Supporting the findings of Harper (1977) and bringing them one step further, Greene and Johnson (1994) argued quantitatively that mean long-term seed production was inversely proportional to seed mass raised to the power -0.58. Likewise for herbaceous plants, Shipley and Dion (1992) showed the same inverse relationship (but with a steeper exponent).

Another factor to consider is the size of the plant. Fowells and Schubert (1956) had earlier shown that canopy trees virtually monopolized seed production. Indeed, Greene (2000) found that basal area density successfully predicted recruit density

($r^2=0.53$). Greene and Johnson (1994) showed that mean annual seed production was proportional to basal area (at least prior to senescence) raised to the power 0.92, while Shipley and Dion (1992) argued that it was proportional to vegetative dry mass raised to the power 1.07.

Finally, one might ask: do taller plants produce more seeds because they have more leaf area or because they receive more light? Holding size constant, Greene *et al.* (2002) found that light does play a role: subcanopy trees suddenly released by harvesting had elevated light levels and comparatively greater seed production than similar-sized conspecifics in the adjacent undisturbed forest.

Seed production varies annually with most species experiencing the marked temporal variation called masting. In a study spanning several years in a deciduous forest near Quebec City, Houle (1994) noted that inter-annual variations in seed abundance and viability were very strong. This trait is primarily controlled by climatic cues in the year of bud differentiation--for trees this is typically the summer prior to flowering (Greene and Johnson, 2004). It may well have evolved as a way of minimizing seed predation losses (Silvertown, 1980). Thus, as Beckage *et al.* (2000) found, seedling recruitment density is strongly linked to seed availability. Species with low seed rain (too few trees and/or a poor seed production year) produced corresponding less dense cohorts of recruits.

Soil seedbanks (the retention of viable seeds in the soil for more than one growing season) are assumed to be of modest importance for tree species in temperate forests because their dormancy-breaking cues are quite modest (Mladenoff, 1990; Matlack and Good, 1990; Schiffman and Carter-Johnson, 1992; Yorks *et al.*, 2000). Nonetheless,

some of the species of interest in my own study certainly have the capacity to bank seeds for a year or two. For example, yellow birch maintains a seedbank (Houle, 1994). Hille de Ris *et al.* (2005) found that red maple seeds may become part of a seedbank, if emergence is delayed in the release season, for up to approximately 15 months, as it would increase chances of survival. It is unlikely though that dormancy extends beyond the next spring (Marquis, 1975 – discussed in Houle 1994). Black cherry seeds may remain viable for up to five years (Marquis, 1975; Burns and Honkala, 1990). Houle (1994) detected no seedbank for beech. As for white ash, striped maple, and sugar maple, it is assumed that they have no multi-year dormancy; they shed seeds in the autumn and these will germinate by the following spring (Burns and Honkala, 1990).

Spatially-explicit models for tree recruitment dynamics have dealt with the seed production in an uncomplicated way. This portion of the recruitment equation can be written as seedling density equals some coefficient (intercept) multiplied by tree diameter raised to an exponent. Thus, if we assume seed production is proportional to basal area (as with Greene and Johnson (1994)), then the exponent for diameter would be 2—a value used by Ribbens *et al.* (1994) and Lepage *et al.* (2000) in the SORTIE recruitment subroutine. (Note that in the next chapter, I will let the exponent vary.) Thus, this very simple approach ignores much of the biology: the same amount of seeds is produced every year by a species (there is no masting) and light receipt has no effect on this mean production. Perhaps the worst feature of this simplicity is that it assumes that tree size really is a good predictor of seed production. But, as shown by Calogeropoulos *et al.* (2003), while it may well be our single best indicator (and certainly the easiest one to

measure), nonetheless tree size within a species at a site typically explains only 10 to 40% of the variation in seed production.

Seed Dispersal

Recruitment of all tree species is limited by seed dispersal at early life history stages (Hille Ris Lambers and Clark, 2003). No matter what the dispersal agent, there will always be some clement sites that are not reached. The main reasons advanced in the literature for dispersal are to escape density-dependent seed and seedling mortality near the parent (Janzen, 1970; Connell, 1971), to colonize disturbances (e.g. small gaps, nearby burns, etc, Baker, 1974), and to find seedbeds suitable for establishment and growth (Howe and Smallwood, 1982). For example, for black cherry, escape from under fruiting parent trees is imperative where a pathogenic pseudo-fungus builds up and kills the seedlings (Packer and Clay, 2000); sugar maple is affected by density dependent mortality (Houle, 1994). Yellow birch experiences dispersal over a more extended period of time (autumn plus winter) than its competitors; this may allow for a broader seed shadow and thus more careful “exploration” of the local environment (Houle and Payette, 1990).

Seed size plays an important role in dispersal (Harper, 1970). Smaller-seeded species should have greater dispersal capacity because small seeds are more readily transported by dispersal agents such as the wind (Venable and Brown, 1988; Greene and Johnson, 1993): seed mass is proportional to terminal velocity and thus inversely proportional to dispersal. For seeds dispersed on the outside of animals, smaller seeds appear to travel farther because they are less readily detected by the animal (Greene and Calogeropoulos, 2002). For dispersal via alimentary canals, however, there is no

evidence that dispersal capacity is inversely proportional to seed size, although which animals take which seeds can of course be affected by the relative size of both seed and vector (Greene and Calogeropoulos, 2002).

Tree height plays a role for wind-dispersed species because (1) trigonometrically, the taller the parent the farther the seed will travel, and (2) taller trees experience greater wind speeds. There is no evidence for a similar effect of height on the distance traveled with animal dispersal.

Secondary dispersal (i.e. further movement after initial contact with the ground) by wind on intact seedbeds is very unlikely (Johnson and Fryer, 1992) because the wind speed will be too low. According to Greene and Johnson (1997), even on snow, secondary dispersal is relatively unimportant within hardwood forests where wind speeds are quite low, and simply impossible in conifer forests. The importance of this secondary dispersal in hardwood stands, however, depends on the percentage of the crop that abscises in winter and the percentage of winter months where snow is present on the ground (Greene and Johnson, 1997). For yellow birch in Québec, Houle and Payette (1990) found that 24% of the crop is deposited on snow.

For animal dispersed seeds however, secondary dispersal by caching rodents and birds may be considerable. Of my two animal-dispersed species, some black cherry fruits will not be consumed, will fall to the ground, and be moved again by rodents. As for beech, most seeds have a primary dispersal event consisting of the wind pushing the massive seeds a few meters laterally away from the parent tree, with subsequent secondary dispersal by rodents and birds. Certainly, rodents generally do not move the

seeds far: typically only a few meters (Sork, 1984). Birds however, (e.g. blue jays) will undoubtedly take them much further away (Johnson and Adkisson 1985).

The simple model of recruitment that I will be using (SORTIE recruitment subroutine) has a dispersal term embedded within it. Ribbens *et al.* (1994) used a two-parameter Weibull, as did Lepage *et al.* (2000). Recently, however, Greene *et al.* (2004) argued that the Weibull was an unlikely function on theoretical grounds, and then showed that the lognormal offered a much better fit for data sets where there was only a single tree (far from any other conspecifics) within the forest, and a marginally better fit for situations such as I will face where we have overlapping dispersal curves (i.e. dense stands of conspecific source trees).

The simple dispersal term in the SORTIE recruitment subroutine does not differentiate between primary and secondary dispersal. That is, at best, we are looking at the net movement away from the tree. A more worrisome problem, especially given that most of my species are wind-dispersed, is that the dispersal term is a constant for all conspecific seeds regardless of source size. That is, small sugar maples for example will have the same dispersal capacity as large sugar maples.

Survivorship as mediated by granivores and seedbeds

Generally, in an average year, approximately half the filled seed crop of northern conifers is lost to granivores and frugivores after abscission (but before germination) (Greene and Johnson 1998), while another large fraction is lost prior to abscission (Silvertown, 1980). As mentioned above, it has now become clear that almost invariably animals prey on seeds in a density-dependent manner in both the tropics and higher latitudes (Greene, 2000; Wright, 2002)

As for seedbeds, survivorship will be directly affected by germinant size, and thus by seed size (which is allometrically related to germinant size). It has been well established that moisture availability is the crucial factor in determining survival during the first few weeks following germination (Duscheneau and Morin, 1999). Greene and Johnson (1998) argued that seedbeds could be grouped into those that are high porosity (e.g. mosses, litter layers) and thus easily lose water in the absence of rain; those that are low porosity (exposed mineral soil, humus, rotted wood) and thus can re-supply water by capillarity from lower layers; and, lethal seedbeds such as firm wood, rocks, or puddles. For the high porosity seedbeds much would depend on the interaction of seedbed thickness and germinant radicle length. Thus, a thin layer of *Polytrichum* moss is no barrier for a tiny spruce germinant that can easily push its radicle into the underlying mineral soil. By contrast, a 6 cm thick layer of feathermosses is far too thick for the spruce germinant but no serious obstacle for the very long radicle of an oak germinant. As has been shown repeatedly, litter removal can increase recruitment by an order of magnitude (e.g. Hatcher, 1966 for yellow birch; Charron and Greene, 2002 for three conifer species).

During the first autumn, a cover of fallen hardwood leaves can “smother” (the forestry term) small germinants such as conifers and yellow birch (Narukawa and Yamamoto, 2003). They find themselves in total darkness the next spring and their subsequent survival is severely compromised. However, by the end of the third summer, the seedlings have become too tall to be affected by leaf fall.

Survival during the first summer is affected much more by seedbeds than by shade tolerance. Leishman and Westoby (1994) showed that larger-seeded species have

increased survival in low light situations, but the explained variance is small. By the second summer, seedbeds have no effect on age-specific survivorship (e.g. Charron and Greene, 2002), and now shade tolerance can play a major role. As Wright *et al.* (1998) pointed out, while substrate type is the most important requirement for first-summer survival, ideal substrates need not coincide with areas better suited for subsequent survival. Shade tolerance becomes more pivotal for trees as shade tolerant species can establish seedlings under their own canopy whereas less shade tolerant species require canopy gaps of various sizes for successful regeneration (Baker, 1949; Forcier, 1975). In what follows, some of my recruits will be in their second summer and certainly ash and black cherry have only a modest tolerance of shade.

In intact forests, fallen logs are somewhat rare (and of course the rotted portions of those logs are even rarer) (Tyrrell and Crow, 1994; Goodburn and Lorimer, 1998; McGee *et al.*, 1999) unless a major disturbance occurred several decades previously (DeLong *et al.*, 1997). Spies *et al.* (1988) found that the area covered by logs in forests in western North America was 9.8% in young stands, 9.3% in old-growth stands and 6.5% in mature stands. Rotted portions are probably on the order of 1-3 % of the forest floor. Exposed mineral soil and exposed humus are usually very rare in intact forests—perhaps less than 1% of the forest floor—except where uprooting of trees in major disturbances has exposed mineral soil. Much more rarely, digging by pigs, bears, and other animals can expose much humus and mineral soil.

The recruitment subroutine in SORTIE first included a seedbed-mediated survivorship term in Lepage *et al.* (2000). This term permits a set of 10 exclusive categories (exposed mineral soil, rotted wood, firm wood, etc). Each quadrat is then

subdivided by the cover percentage of each type, and of course the total number of recruits within each quadrat is recorded. There are a number of problems with this approach. First, correlation between seedbeds is ignored. For example, portions of rotted wood on fallen logs tend to be adjacent to portions of firm wood with the former giving rise to many yellow birch germinants while the latter is barren. The inverse modelling approach will conclude that rotted wood is a good seedbed, but firm is not too bad. Another problem is that the model ignores density-dependent losses to granivores. This reminds us again that we are never looking at primary dispersal curves but rather *realized* curves that include primary dispersal, secondary dispersal, and density-dependent losses which are concentrated near dense groups of conspecific trees. The third problem is that the model assumes light does not matter. This is probably reasonable for the first summer even for very intolerant species, but certainly it is less likely to be true for the second-summer stems that I occasionally use.

Selection Harvesting

In recent years, the objectives of forest management have increased from the classical optimization—how to maximize wood volume/area/time/cost—to include other goals, such as maintenance of biodiversity and ecosystem viability (Seymour and Hunter, 1999). Partial cutting creates intermediate-sized canopy gaps (gaps resulting from harvesting one to several canopy trees) (Beckage et al. 2000). Selection cutting was first applied in Québec on an experimental basis in the early 1980's (Majcen 1994; Bédard, 2001). Selection cutting allows for a continuous forest cover when viewed from a distance, is more aesthetically pleasing and thus was quite popular in the study area

(Eastern Townships). In Québec, the maximum allowable harvesting intensity for selection cutting is 35% of the basal area.

Selection cutting, because it involves harvesting individual stems throughout a stand, requires the installation of forest roads and skid trails. The amount and type of soil disturbance resulting from skidding operations depends on several variables, such as size and type of logging machines, season of harvest, soil type and experience of the loggers (Martin, 1998; Gullison and Hardner, 1993). Haul roads are constructed with heavy equipment and connect the main roads to the skid trails. They are primarily travelled by semi-trailers. Skid trails are travelled by forwarders and skidders (equipment used for harvesting) and are used to move logs from the point of felling and bucking to log landings. Few improvements are made to skid trails apart from the clearing of a few trees (Buckley *et al.*, 2003). In a northern hardwood forest, Buckley *et al.* (2003), found that skid trails comprised up to 22% of the areas sampled. They also noted however, that canopy cover was not significantly different on skid trails than in areas with no soil disturbance (i.e. skid trails are quite narrow relative to the crown diameters of the residual trees above), but soil compaction and exposed mineral soil was significantly greater in skid trails. This would mean that while harvesting increases the presence of favourable seedbeds, there is not significantly more light available in the understory and the soil becomes somewhat compacted. This leads to the question: what species would be favoured under these conditions? Intolerant small-seeded species or tolerant, larger-seeded species?

Single tree selection cutting and diameter-limit harvesting are used to regenerate very shade-tolerant species such as sugar maple (Crow and Metzger, 1987; Smith and

Miller, 1987; Schuler and Gillespie, 2000; Nyland, 1996). In a study spanning fifty years, Schuler (2004) noted that single tree selection cutting and reference stands resulted in a notably decreased diversity, with a significantly different pattern than was initially present. This is further supported by Beckage *et al.* (2000) who found that intermediate sized canopy gaps were not able to maintain species diversity in second-growth forests.

Emphasizing the importance of shade tolerance, Beaudet and Messier (2002) determined that after 15 years the difference in both canopy openness and pattern of light transmission between partial cut blocks and uncut blocks was minimal. The seven species of interest in this study range from moderately tolerant (black cherry, yellow birch, red maple, white ash) to extremely tolerant (sugar maple, beech, striped maple) (Baker 1949). We would expect that the more shade tolerant species would be more prevalent following partial harvesting. Bédard (2001) noted that sugar maple benefited in all blocks from selection harvesting. Buckley *et al.* (2003) noted that yellow birch seedlings were abundant in haul roads (where we can presume there was exposed mineral soil, and these tiny germinants would benefit accordingly: Godman and Krefting, 1960; Bormann *et al.* 1970; Forcier, 1975). They also noted that 4 to 6 years following a cut, the density of trees in haul roads decreased; they speculated this was due to competition with dense herbs and/or compacted soil.

Modelling

The need for sustainable forest management is imminent given the increasing demands for consumptive and non-consumptive forest uses. Sustainability was a simple issue so long as we sought monocultures of planted, tended stems grown for short rotations: i.e. the agricultural model of classical forestry (Coates *et al.*, 2003). But given

the increasing emphasis on polyculture and multiple use—and given that partial cutting, the great exception within forestry, always aimed to maintain diversity among (at least) the shade tolerant fraction of the forest—we need to understand the complex changes that our interventions cause in the subsequent dynamics. Given the rarity of long-term studies on vegetation dynamics, simulation modelling is a useful means of inferring forest dynamics (Busing and Mailly, 2004). Several models are available that attempt to predict forest dynamics.

Models, very broadly defined, have been available since the start of the last century. Early models of dynamics, such as that proposed by Clements (1916) with the climax theory, were merely verbal. More quantitative ideas appeared in the 1960s and 1970s, with those of Forcier (1975) and Horn (1975) using matrices. These were superseded by FORET-type spatial models (Shugart and West, 1977; Ek and Monserud, 1974) that pictured a single space called a “gap” in which dynamics took place. These dynamics were dependent on the matrix in which the space was embedded for some processes (e.g. if there were many sugar maple around the gap, then there would be a greater amount of sugar maple seeds deposited into the gap) but not for others. In any case, there were no spatially-explicit connections (processes) between individual trees and that space of interest. Once personal computers became available in the early 1980s, spatially realistic stand dynamic simulations began to supplant these earlier approaches. The purpose of these models is to extrapolate from measurable fine-scale and short-term interactions among individual trees to large-scale and long-term dynamics of forest communities (Pacala *et al.* 1996). The newer models combine at least 3 subroutines, as

does the SORTIE model, which contains 4 (Pacala *et al.* 1996). The focus of this paper is the recruitment subroutine. The other subroutines are light, growth, and mortality.

Regeneration is certainly one of the essential processes that maintain the stability and species coexistence in mixed forests (Fox, 1977; Runkle, 1981; Nakashizuka, 2001). Inverse modelling represents a “powerful” method of estimating fecundity and dispersal (Ribbens *et al.*, 1994; Clark *et al.*, 1998). Inverse modelling is used when observations are noisy, incomplete and irregular and parameters cannot be measured directly. It performs parameter estimations using a maximum likelihood (method of least squares) analysis and requires assumptions to be made in order to predict how a system behaves. It applies Bayesian theory to determine the best-fit parameters. SORTIE’s recruitment subroutine uses an equation in combination with Cartesian co-ordinates, sizes of source plants and the coordinates of progeny to estimate the parameters within the dispersal term (Greene and Calogeropoulos, 2002). The three main processes wedded in a single function govern seed production, dispersal, and survivorship.

Perhaps the best way to produce better models and gain a more in-depth understanding of forest dynamics, is to make careful comparisons of the assumptions and predictions of existing models with empirical data (Robinson and Ek, 2000; Busing and Mailly, 2004). This thesis is intended to make a contribution to that evaluation.

EVALUATING SORTIE'S RECRUITMENT SUBROUTINE

INTRODUCTION

Understanding recruitment in any given forest type is crucial to achieving sustainable forest management (Lepage *et al.*, 2000). To do this we need to comprehend how many seedling recruits are produced by an adult (i.e. its fecundity) and how these recruits are dispersed away from the maternal parent. The challenge lies in the fact that different species use varying reproductive strategies which are subsequently affected by their environment. There are great differences in seed production, seed dispersal, and juvenile survivorship among species. Survivorship is mostly dependent on substrates and granivory. Past research has tended to narrowly focus on one of the functional relationships affecting tree recruitment independently of the others (e.g. Greene and Johnson, 1994 for seed production; Greene and Johnson, 1996 for seed dispersal; Greene and Johnson, 1998 for survivorship; Wright *et al.*, 1998; Beaudet *et al.*, 2002 for light transmission; Erickson and Ehrlen, 1992; Coates *et al.*, 1997 for seedbeds; Kobe *et al.*, 1995 for shade tolerance). Starting with Ribbens *et al.* (1994), there have been a few recent attempts to meld these functions into a single, spatially realistic recruitment model that is based on minimal field measurements and inverse modelling (Clark *et al.*, 1998; Greene *et al.*, 2004).

Seeds represent a common way that trees reproduce (Harper, 1997) and thus size and quantity of seeds produced will have a profound effect on the fitness of a species. Quantifying seed production has been difficult because plant species differ in the proportion of the net annual assimilated income devoted to reproductive effort (Struik, 1965; Ogden, 1968) and this may also vary intraspecifically from year to year: e.g.

masting. Further, individuals within a species differ in seed production. On an individual level, Greene and Johnson (1994) argued that the number of seeds produced was an inverse function of seed size and a positive function of tree size, specifically basal area. However, this can only be assumed to be true for canopy species as lower light intensities may result in reduced seed production (Greene et al. 2002). The largest individuals (those we would predict to produce the most seeds) are in the canopy and receive the most light. In this study I will, however, assume that the same tree size-production relationship holds for both the canopy and subcanopy, given that selection harvesting has taken place in all sites and has consequently opened up the canopy slightly allowing for more light transmission than would be present in an intact forest.

A trade-off occurs in seed production in trees. Harper (1970) noted that seed number versus seed size are necessary trade-offs (although a completely reciprocal relationship cannot be expected) and yet he could not determine (Harper, 1977) an obvious trade-off. Shipley and Dion (1992) demonstrated the inverse relationship for herbs, and this was followed by Greene and Johnson (1994) who showed that larger-seeded species produced fewer seeds than small-seeded species. Both Greene and Johnson (1994) and Ribbens *et al.* (1994) argued that seed production should be proportional to the square of tree diameter i.e. to basal area.

Although vegetative reproduction permits fast initial growth and thus increases chances of survival into adulthood, this form of reproduction is not conducive to the rapid spread of trees (Harper *et al.*, 1970). Trees use their seeds in order to invade new sites as well as to fill canopy gaps in their immediate locale. The size of the seed in wind dispersed species will have a deciding effect on how far they can go and affect the shape

of the dispersal curve. Species producing small seeds should have greater vagility than their larger-seeded counterparts, at least when wind is the vector (Greene and Johnson, 1993; Greene and Calogeropoulos, 2002; Venable and Brown, 1988). However, their successful establishment will likely be more affected by environmental factors such as microsite constraints (DeLong *et al.*, 1997; Greene and Johnson, 1998).

Seed dispersal patterns are a critical component of spatial variation in plant seedling recruitment (Ribbens *et al.*, 1994). The shape of the dispersal curve has been the subject of much debate in recent years and is hard to observe empirically given the overlapping curves of adjacent conspecific seed sources within forests. Isolated point source (single tree) studies in a clearing will not accurately mimic dispersal dynamics in a forest (Clark *et al.*, 1999). To predict recruitment, Ribbens *et al.* (1994) used the two-parameter Weibull dispersal curve; Clark *et al.* (1998) used a modified t-distribution, which they called a 2Dt, and Greene *et al.* (2004) preferred the lognormal. As Greene *et al.* (2004) indicate for point sources, the Weibull forces too many recruits to be located in very close proximity to the parent and creates a fore-shortened tail and is thus unrealistic. Clark *et al.* (1998) suggested that, although it tends to place too many recruits too far from the parent tree, the 2Dt was a better alternative to represent both the near and far end of the curve. As Greene *et al.* (2004) pointed out, the 2Dt provides unlikely results (excessively high mean dispersal distances are commonly calculated). In this study, I used the lognormal and the Weibull dispersal functions. The latter was included in order to allow for comparisons with dispersal parameters published in Ribbens *et al.* (1994) for the species common between the two studies.

The ability of a viable seed to successfully germinate and survive the first few months is contingent upon temperature, moisture, substrate porosity and avoiding predation. Aside from the latter factor, this list can be subsumed as characteristics of the seedbed. Smaller seeds have more exacting seedbed requirements than larger seeds because small seeds necessarily create small radicals and are incapable of penetrating deeper substrates such as leaf litter. Likewise, small seeds produce short hypocotyls that cannot push a thick layer of fallen leaves aside. The best seedbeds available to small-seeded species are exposed mineral soil, exposed humus, elevated rotted wood (because it sheds leaves) and, in lowlands, *Sphagnum* mosses (Lees, 1963; Groot and Adams, 1994; Greene and Johnson, 1998; Greene *et al.*, 1999). Further support is offered by Calogeropoulos *et al.* (2004), who noted in two small-seeded species that disturbed soil surfaces such as mineral soil or humus improved juvenile survivorship by more than an order of magnitude over that of intact litter seedbeds.

Seed predation may substantially reduce the effective reproductive output of a plant (Harper *et al.*, 1970; Silvertown, 1980; Greene and Johnson, 1998). In the southern boreal forest of Québec where plots were caged to exclude rodents or left open to allow granivory, Simard (1999) found that the granivory rate was 0.80. Greene & Johnson (1998) in their review of the literature found an average of 0.58. These large rates of seed predation offer further support for studying seedlings rather than seeds when attempting to predict forest dynamics in areas other than those that have been ravaged by fire where the granivores would have been temporarily removed.

Given that recruitment is a crucial stage in forest regeneration following logging (LePage *et al.*, 2000) and thus the renewal of a valuable resource, ecologists as well as

foresters have developed an interest in the use of stand dynamics models to predict forest dynamics in order to regulate harvests to insure no detrimental effect on the land. A parameter estimator uses inverse modelling to estimate parameter values for a subroutine (presently the recruitment subroutine of SORTIE) based on field measurements. Inverse modelling involves comparing seedling densities in Cartesian space with the spatial coordinates and sizes of potential source trees to arrive at best fit parameter estimates. SORTIE is a spatially explicit mechanistic model that predicts forest dynamics at the stand level, where each individual tree plays a role in relation to its size and location. It was initially conceived to predict natural stand dynamics, but has recently been modified to allow the user to predict the effects of different harvest types and intensities. It is composed of 4 subroutines: Light, Growth, Mortality and Reproduction. This research project uses the reproduction subroutine of SORTIE initially developed by Ribbens *et al.* (1994) and subsequently modified to include seedbed effects by Lepage *et al.* (2000). The equation used in the recruitment subroutine is:

$$(1) \quad F_{(x,y)} = \text{STR}(\text{DBH}/30)^\alpha f(x) \sum p_i f_{i(x,y)}$$

where $F_{(x,y)}$ is the recruit density in a given quadrat ($\#/m^2$); STR (standardized total recruits) is the potential number of seedlings produced by a parent tree with a diameter at breast height (DBH) of 30 cm; α modifies STR as a power function of the actual DBH observed, in other words, it translates tree size into recruit production (This first part of the equation implicitly includes seed production and the averaged loss to granivory); $f(x)$ is the dispersal term; p_i is the proportional cover of the i^{th} substrate type; and, $f_{i(x,y)}$ is the

favourability of the i^{th} substrate. The search radius applied (i.e. how far we searched for parent trees) was set at 200 m throughout the simulations. In order to determine the value of the parameters to be used, one can either estimate values from what is known and published or values can be calculated based on field measurements. Here, I will estimate parameter values using field data and a parameter estimator.

Where LePage *et al.* (2001) compared values obtained for SORTIE for forests that were exposed to different harvest treatments, I have used the parameter estimator to provide values for selection cuts only. In selection cut or partial cut treatments, between 25 and 35% of the basal area is removed by removing either single stems or small groups. An area is designated for the cut and marking is either done ahead of time or the machine operator selects stems as the cut proceeds. The skidder-forwarder enters the area and creates skid paths which are the narrow trails the machines will follow in an attempt to minimize damage to the remaining stems. From these skid paths, machines will reach up to 50 meters into the forest and harvest selected stems. Selection cutting is currently the most popular harvesting technique applied in southeastern Québec.

OBJECTIVES

Verifying the validity of previous research and theoretical predictions will improve the quality of work done in any given field. The objectives of this study are as follows:

- (1) To determine the most accurate parameter values to be used in equation (1) for each of the seven species of interest and, therefore, predict patterns of recruitment in areas where selection harvesting has taken place in southeastern Québec;
- (2) To determine which dispersal function (Weibull or lognormal) results in the highest likelihood values and to compare the results with those published by Greene *et al.* (2004) and those of Ribbens *et al.* (1994);
- (3) To examine the amount of variation among sites for a single parameter for a given species and to determine how much variation exists among species; and
- (4) To determine the relationship between seed mass and seedbed favourability.

METHODS

Study Area

The study sites are located in southeastern Québec within 100km of the city of Sherbrooke (Fig. 1). They are located in the Sugar Maple – Basswood zone, in the ecological sub-region 2cT and landscape unit #8 of Robitaille and Saucier (1998). Located around 45°26'N, 071°41'W, the mean annual temperature in the area is 4.5 °C, mean annual precipitation is 1111 mm (of which approximately 25-30% falls as snow) with a relative humidity of 73.9% (The Weather Network – these data covers a 30 year sampling period from 1961-1990). The sites consist of mesic, sugar maple-dominated northeastern deciduous forest that have recently been partially harvested using single and multiple-tree selection cutting, have a drainage rating between 2 and 3 (in Québec sites are ranked between 0 and 6 where 0 is the driest and 6 the wettest), and contain at least five of the seven species of interest. These stands are generally on the order of 70-110 years old according to Domtar inventories (Domtar is a pulp and paper company that owns a lot of land in southeastern Québec). Presumably, they represent second growth forests following the spate of harvesting of the old growth hardwood and pine stands in the period 1890-1940 in this area (D.F. Greene, unpublished data). The seven species of interest in this study are striped maple (*Acer pensylvanicum*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), beech (*Fagus grandifolia*), white ash (*Fraxinus americana*), and black cherry (*Prunus serotina*). Other species included hemlock (*Tsuga canadensis*), butternut (*Juglans cinerea*), ironwood (*Ostrya virginiana*), and basswood (*Tilia americana*) each representing less than 1% of

the basal area. Only sexual recruits were included in the study. Over a two year period, four sites were sampled (StoSC2001, SutSC2001, SutSC2002, WeeGSC2001) , two in 2002 (Stoke and Sutton) and two in 2003 (Sutton and Weedon) where species composition varied between sites with some species not being present in some areas; sugar maple (38-69%), beech (12-25%) and yellow birch (9-22%) consistently represented the bulk of the basal area. All sites were harvested either one or two years before sampling. See Table 1 for a summary of site characteristics.

Field Data

Recruitment data were collected from September to early November 2002 and June to July 2003 in 10 belt transects located in selection cuts at least 30m from a logging road and a minimum of 100m from another transect. Each transect crossed a skid path at approximately ninety degrees, and was composed of 50 consecutive 1m² plots (Fig. 2). For every plot, recruits (germinants up to and including 2 year olds – 2 year olds are in there second growing season) were aged and identified to species. No recruits older than two years old were included in the study in order to minimize the inclusion of offspring of harvested trees in the analyses. The proportions of various seedbed types were recorded for each 1m² plot as a percent cover using a 1% grid as a reference. Five categories of seedbed were used:

(1) Mineral soil / humus / moss: exposed mineral soil or organic material (humus) present as a result of logging activity or wind throw or *Polytrichum* or any other moss in a sufficiently thin layer that it would not retard germination. Leaf litter less than 3 cm was also placed into this category.

- (2) Leaf litter: a thick (≥ 3 cm) layer of undisturbed plant material (including intact or partly decomposed leaves). Moss ≥ 3 cm thick (very rare) was also placed in this category.
- (3) Rotted wood: wood sufficiently decomposed that it was qualitatively judged to be a potential germination substrate. i.e. soft enough that it broke apart easily.
- (4) Fresh wood: recently felled trees or stumps often due to logging activity or windthrow or branches with a minimum diameter of 1cm.
- (5) Rocks.

All potential parent trees within 50m of each transect were mapped. Spatial coordinates and diameter at breast height were recorded for each potential parent tree greater than 8cm in DBH (5cm DBH for striped maple). Spatial coordinates were determined using a compass and an Impulse LaserRange Finder. In all, 15 ha, 1.5 ha per transect, were mapped. The breakdown of transects per site is as follows: three transects were installed in 2002 at Stoke in the 2001 selection cut block; five transects were installed at Sutton, three in 2002 in the 2001 selection cut block and two in 2003 in the 2002 selection cut block; and, three transects were installed in 2003 in the 2001 group selection cut block at Weedon.

For white ash, a dioecious species, I attempted to minimize the inclusion of male trees by using binoculars to determine whether or not seeds were present on the tree.

Parameter Estimation

Equation (1) (p.18) is the basis for the parameter estimator. The data were subsequently analyzed using a parameter estimator program that seeks the maximum likelihood for Equation (1). I ran the program using two different dispersal functions, the

2-parameter Weibull and the lognormal. The corresponding dispersal terms ($f(x)$ in equation (1)) are as follows:

$$(2) \quad f(x) = e^{(-dx^\theta)/n} \quad (\text{Weibull})$$

where x is the distance from the parent tree (m); d determines the rapidity of the decline in recruit numbers as the distance from the parent tree increases, θ determines the shape of the distribution, and n is a normalizer required to make $f(x)$ sum to 1.0 when multiplied by $2\pi x$ (one would multiply by $2\pi x$ to determine seedlings per annulus).

$$(3) \quad f(x) = [e^{-(\ln(x / x_{0.5})^2 / 2\sigma^2)}] / (2\pi)^{1.5} x^2 \sigma \quad (\text{lognormal})$$

where $x_{0.5}$ is the median dispersal distance, and σ determines the shape of the distribution. See Figure 2 for a depiction of the two dispersal curves.

Using the Weibull function, the program was run four ways: all parameters were allowed to vary; α was set at 2 (as recommended by Greene and Johnson, 1994 and Ribbens *et al*, 1994) and θ was allowed to vary; α was set at 2 and θ set at 2; or, α set at 2 and θ set at 3. The lognormal was run two ways, allowing the σ and $X_{0.5}$ to vary and α to either vary or be set equal to 2. Note that for all simulations the favourabilities of seedbeds 1 through 3 were permitted to vary between zero and one, while the favourabilities of seedbeds 4 and 5 were set to zero. Parameters were obtained for each site by pooling the transects at one site (two transects at WeeGSC01 and SutSC02 and three transects at SutSC01 and StoSC01).

Statistical Analysis

Given the parameter estimates, the correlation between the predicted and observed recruit density was used to judge the significance of the model. The Weibull and the lognormal functions were compared using the log-likelihood values. A log-

likelihood value is significantly different from another if the difference between them is greater than the critical χ^2 value for one degree of freedom (3.84). The accuracy of the predictions was tested through regression analysis (i.e. is the slope of the regression for observed versus predicted significantly different from 1.0?). The amount of variation among species for a single parameter was tested (ANOVA) for the instances where all parameters were permitted to vary. The relationship between seed mass and favourability was determined using regression. The values of the seedbed favourabilities generated by the program for both mineral soil/humus/thin moss and rotted wood were divided by the values generated for leaf litter to create ratios. This allowed me to compare the $f_{i(x,y)}$ of sites and species which cannot otherwise be compared directly due the variation in the proportions of seedbeds present. Seedbed favourability values with 5% confidence limits that varied between zero and one (recall that these values are the upper and lower limits for this parameter) were excluded from analysis.

RESULTS

Given the number of species and sites for which there was sufficient data to allow for the estimation of parameter values, I obtained results for 19 sets of species and sites. These maximum likelihood estimates of parameters are presented in Table 2 (a through e).

A priori determination of α and θ values

All correlations between observed and predicted (r^2) proved to be significant ($p < 0.05$) when α was allowed to vary with either dispersal function (Table 3). (Recall that α is the parameter that translates tree size – diameter – into recruit number.) With α

fixed at 2.0, there were three insignificant correlations for the Weibull and one for the lognormal. When I imitated Ribbens *et al.* (1994) and not only fixed α at two but also the shape parameter, θ , at 3, the number of insignificant correlations was three for the Weibull.

Setting α to two had a dramatic effect on θ in only five instances. When other parameters were allowed to vary and α was set to two, θ was significantly different from three (the value recommended by Ribbens *et al.* (1994)) seventeen times and only similar twice based on 95% confidence intervals (Appendix I). Setting α to two resulted in higher values of d than allowing it to vary for beech, black cherry, red maple, sugar maple and yellow birch (Appendix II). Also, α was not significantly different from 2.0 (the previously recommended value) only once for both the Weibull and the lognormal (Appendix IV).

Comparison of the two dispersal functions

The lognormal proved to be a better model than the Weibull. When either α was allowed to vary or was set at 2, the lognormal had a higher log-likelihood than the Weibull in seventeen out of nineteen simulations. Of these, the lognormal was significantly better (χ^2 test) in twelve of nineteen when α could vary, and eleven of nineteen with α fixed at two. Two of the simulations where the Weibull resulted in a higher likelihood occurred for beech, once at SutSC02 and once at Weedon; at Stoke, the Weibull was better for yellow birch and at SutSC01 it was better for striped maple. The Weibull was never a significantly better predictor at the individual sites, yet when all sites were lumped together, the Weibull was significantly better both times it outperformed the lognormal (Table 4).

One also expects that a good model would not merely provide a high correlation, but also a slope of 1.0 with observed regressed on predicted. With all parameters permitted to vary, the lognormal produced only two correlations between observed and predicted that had a slope significantly different from one (t-test; $p < 0.05$). By contrast, the Weibull produced five slopes significantly different from one.

In summary, the lognormal proved to be a much better predictor than the Weibull. This was true whether the parameters were fixed or varied.

Variation in parameter values among species and sites

The shape parameter, θ , of the Weibull, varied considerably among species as well as within species at different sites (Appendix I). For example, with α permitted to vary, θ varied from 0.3 to 4.88 for sugar maple (4 sites), 2.2 to 2.4 for beech (3 sites), 0.06 to 4.7 for striped maple (3 sites), and for yellow birch 1.0 to 4.8 (4 sites). In short, there was no species effect (ANOVA; $p = 0.638$).

The shape parameter of the lognormal, σ , showed similar trends for variation among and within species. For example, with α permitted to vary, σ varied from 0.21 to 0.96 for sugar maple (4 sites), 0.08 to 0.96 for beech (3 sites), 0.09 to 1.5 for striped maple (3 sites), and for yellow birch 0.01 to 0.49 (4 sites). Given the amount of variation within species, there was not any significant difference in σ among species (ANOVA; $p = 0.594$). Greene *et al.* (2004) recommended a value of $\sigma = 1.0$. For only two of nineteen (α vary) simulations was there no significant difference between σ and 1.0 and in the vast majority of cases, values were lower than 1.0; and σ was always significantly different from 1.0 when α was set to 2.0 (Appendix I).

There was variation in d (the location parameter for the Weibull) both among species and within (Appendix II); however, there appeared to be a tendency toward species-specific values (ANOVA; $p = 0.005$). Black cherry tended to have the largest d values (2 sites) and yellow birch tended to have the smallest (4 sites). There appeared to be more variation both among species and among sites within a species for the location parameter of the lognormal, $x_{0.5}$ (the median distance) (Appendix II). The median dispersal distance, when α was allowed to vary, ranged between 2.3 and 10.3 for sugar maple (4 sites), 13.4 and 54.4 for yellow birch (4 sites), between 17.1 and 2302.6 for striped maple (3 sites), and 5.5 and 100.9 for beech (3 sites). There was no significant difference among species (ANOVA; $p = 0.594$).

Jointly, the shape and location parameters determine the mean dispersal distance (MDD). MDD values from the Weibull simulations showed no significant species effect (ANOVA; $p = 0.701$). MDD values tended to be low for beech (5.8 to 9.0, 3 sites), black cherry (11.6 to 25.5, 2 sites) and sugar maple (5.0 to 9.9, 3 sites - this excludes one site that had an MDD of greater than 50000m), intermediate for striped maple (19.4 to 43.0, 3 sites - this excludes one site with an MDD greater than 50000m), and higher for red maple (93.7, 1 site), white ash (104.8, site - excludes another site that had an MDD of greater than 50000), and yellow birch (18.2 to 351.1, 4 sites) (see Appendix II). Using the lognormal, there was a stronger species effect, but it was still insignificant (ANOVA; $p = 0.192$). Values tended to be low for black cherry (3.3 to 36.3, 2 sites) and sugar maple (5.0 to 11.0, 4 sites), and higher for beech (21.4 to 102.1, 3 sites), red maple (56.0, 1 site), striped maple (17.6 to 173.1, 3 sites), white ash (47.3 to 479.6, 2 sites), and yellow birch (19.2 to 55.3, 4 sites) (Appendix III). Also to be noted is the fact that MDD values

tended to fluctuate (both up and down) depending on which dispersal equation was applied (Appendix III).

The α parameter was allowed to vary in simulations with both the Weibull and the lognormal (see Appendix IV). For the Weibull, it ranged from 0.02 to 8.5 for sugar maple (4 sites), from 0.006 to 8.1 for yellow birch (4 sites), 0.005 to 4.6 for striped maple (3 sites) and 2.7 to 6.0 for beech (3 sites). With the lognormal it varied from 0.02 to 7.7 for sugar maple (4 sites), from 0.006 to 7.7 for yellow birch (4 sites), 0.05 to 4.6 for striped maple (3 sites) and 2.9 to 6.0 for beech (3 sites). Both the range of values for all species and for each individual species were very similar no matter which dispersal function (Weibull or lognormal) was used and that there was no significant difference in α values between species ($p=0.268$ for Weibull and $p=0.076$ for lognormal).

The STR values obtained using the Weibull (α varying) tended to vary more among species than within (Table 9 (a)), with a stronger contrast for the lognormal (ANOVA; $p=3.23 \times 10^{-5}$) than from the Weibull (ANOVA; $p=0.003$). Some examples of the STR values obtained using the Weibull when α was allowed to vary for sugar maple (4 sites) were 3.3 to 4881.6, for yellow birch (4 sites) were 1092 to 62703, for striped maple (3 sites) 39310 to 94321, and for beech (3 sites) 22.3 to 218.2. Some examples of STR values obtained using the lognormal were sugar maple (4 sites) 8.9 to 553.3, for yellow birch (4 sites) 865.1 to 49520, for striped maple (3 sites) 81782 to 96043, and for beech (3 sites) 480.6 to 2096.0 (Appendix V). Generally, the Weibull and lognormal gave STR values within about two-fold of one another but there were some strong exceptions (e.g. beech).

I also compared the MDD and STR values I obtained with those of Ribbens *et al.* (1994) setting $\alpha=2$, $\theta=3$ as in that paper. Using a random block design I compared the five species that were common between two of my study sites and the Ribbens *et al.* (1994) data, namely beech, black cherry, sugar maple, white ash and yellow birch. For MDD, there was no significant difference between sites ($p=0.349$) however, there was a significant difference between species ($p=0.011$). For STR, there was no significant difference between sites ($p=0.309$) or between species ($p=0.406$). In other words, when the same approach is used, I generally supported the findings of Ribbens *et al.* (1994).

Seedbeds

The seedbed coverage, averaged across all transects were leaf litter (78%), mineral soil/humus/moss (11%), fresh wood (7%), rotten wood (2.5%) and rock (1.5%) (Figure 4). For all ten transects leaf litter was always the most common seedbed while rotten wood and rock were the rarest (Figure 5). The site with the most exposed mineral soil/humus was SUTSC02 transect 2 (Figure 5). SutSC01 was the site with the highest proportion of favourable seedbeds.

The favorability values generated by the program (see Appendix 6) were used to create ratios of the favourability on mineral soil/humus/moss to the favourability on leaf litter, as well as the favourability on rotten wood to that on leaf litter. Recall from the Methods section that we cannot directly compare calculated favourabilities from one site to the next, even within a species because the relative availabilities of seedbeds vary among sites. We can however compare ratios of favourabilities. Further, these favorability ratios will be identical to the ratios of the unknown absolute species-specific survivorships associated with the same seedbeds. Figure 6 shows the relationship

between these two favorability ratios and seed mass (grams) on a ln-ln plot. When the proportion of good seedbeds (mineral soil, rotten wood) is high, smaller-seeded species are present and larger-seeded species don't tend to occur. When the ratio is low (e.g. more leaf litter) none of the smaller seeded species occur and the larger seeded species are present. The regression of the ratio of mineral soil to leaf litter versus seed mass was, as expected, significantly negative ($p=3.99 \times 10^{-8}$, $r^2=0.32$). While the slope was also negative for the regression of rotten wood/leaf litter versus seed mass, the relationship was not significant (Figure 6; $p=0.224$).

DISCUSSION

A priori determination of alpha values

Not surprisingly, allowing α to vary always resulted in the highest likelihoods and all regressions of observed versus predicted were significant for both dispersal functions; in two cases the slope was significantly different from 1.0 for the lognormal, whereas the Weibull had five that were significantly different from 1.0. These deviations from 1.0, for the lognormal, occurred for striped maple at Stoke as well as white ash at SUTSC02. It should be noted in the case of striped maple, that the slope was also significantly different from 1.0 when using the Weibull and thus, the problem probably lies with the species at that site not fitting any curve particularly well. One possible explanation is the patchy distribution of the species at that location. In the case of the dioecious white ash, perhaps the inclusion of some male trees in the analysis had an effect.

The parameter that translates tree diameter into reproductive output, α , has previously been set to two as suggested by Ribbens *et al.* (1994) and Greene and Johnson

(1994). While my results supported the argument for a positive relationship as discussed by Greene and Johnson (1994), 2.0 is not some ideal value. Using the Weibull, α was not significantly different from 2.0 only once (and once when all sites were run simultaneously), it was significantly greater thirteen times (four times for all sites pooled), and significantly less five times (twice for all sites pooled). When the lognormal was run, α was not significantly different from 2.0 once (zero times for all sites pooled), it was significantly greater thirteen times (three times for all sites run simultaneously) and was significantly less five times (four times for all sites together). As with the other parameter, there seems to be no useful default value I can suggest for any one or for all species.

Comparison of the dispersal functions

My results indicating the lognormal is a better model for seedling dispersion than the Weibull supported the findings of Greene *et al.* (2004). These two studies lend strong support to the discontinuance of the Weibull in modelling seedling dispersion. The simulations where the Weibull significantly outperformed the lognormal occurred only when all sites were pooled. It is not at all obvious why its relative performance would improve with site pooling.

Variation in parameter values among species and sites

Regarding the shape parameter for the Weibull, θ , we saw that there was tremendous variation and no species effect. The value for θ (3.0) suggested by Ribbens *et al.* (1994) and used by Lepage *et al.* (2000) was not supported by this research as seventeen out of nineteen times the value determined by the simulation was significantly different from 3.0, both when α was allowed to vary and when it was set at 2.0. When α

was allowed to vary, θ was actually significantly less than 3.0 twelve times and significantly greater five times. Conversely, when α was set at 2.0, θ was significantly less than 3.0 seven times and greater ten times. There appears to be no consensual value I can recommend for any single species, let alone all species. Given this pattern I expected to see a relationship between α and θ , however no relationship was found upon testing.

Turning to the shape parameter for the lognormal, σ , Greene *et al.* (2004) suggested 1.0 as its value given studies of point sources (single trees) within forests. I saw that when α varied, in seventeen of nineteen trials it was significantly less than 1.0; and, was not significantly different from 1.0 twice. When α was set at 2.0, σ was significantly less than 1.0 in eighteen of nineteen and significantly greater than 1.0 once. My results indicate, therefore, that for these species at these sites the number should actually be lower than 1.0.

There was so much variation in the parameter estimates of the model, the location parameter for the lognormal, $x_{0.5}$, did not have a tendency toward species-specific values. Setting α to two resulted in higher $x_{0.5}$ values than allowing it to vary. This result is worrisome since this is the one parameter that physical theory should allow us to predict for the wind-dispersed species (at least) according to Greene *et al.* (2004).

By contrast, the location parameter for the Weibull, d , resulted in species-specific values. Further, in a general way, these values tended to follow one's intuition with larger-seeded species having bigger values and smaller-seeded species having smaller values. For six of the seven species, allowing α to vary produced higher d values than setting it to two. The exception was yellow birch, where in half of the sites it followed the same pattern as the other species, but at the other sites, the opposite relationship

arose. It should however be noted that whatever happened to the d value, the opposite happened to the θ and so perhaps these differences can be attributed to two different approaches the parameter estimator can take i.e. both a large θ and a large d will shorten the mean dispersal distance.

For the mean dispersal distance, MDD, it is apparent that there was a stronger species effect in the lognormal trials than in the Weibull although neither was significant. The lack of a species effect for the Weibull was clearly a result of the program generating parameter values that resulted in some MDDs of more than 50 km. This happened to four different species (twice for sugar maple) and at least once at each site. At the least this implies that there was not a problem with the data at one isolated site; it instead indicates a problem with the dispersal function. If we exclude these extremely high values, we see what we would expect with the larger-seeded species tending to have smaller MDDs than their smaller-seeded counterparts. As for the lognormal results, we see a similar trend except beech had much higher values than I would expect (assuming only rodents and gravity dispersed the recruits I examined).

Comparing my MDD values with Ribbens *et al.* (1994), I found that while there was a significant difference between species, there was no significant difference between sites (treating the Ribbens data set as an extra site) indicating that the MDD values I found are, in some rough sense, similar to those of Ribbens *et al.* (1994). Note however that a Spearman rank correlation of the MDD values of Ribbens *et al.* (1994) with mine (pooled sites) was not significant ($N=5$; $p=0.505$). Likewise, although they do not mention this, Greene *et al.* (2004) found different values than Ribbens *et al.* (1994) for the 8 species they had in common. For example, they reported a MDD of 65.8 m for *Tsuga*

canadensis whereas Ribbens *et al.* reported an MDD of 4.48 m. In short, we have no successful validation of the MDD values used by Pacala *et al.* (1996) in their stand dynamics simulation.

I also compared my STR values with those of Ribbens *et al.* (1994) and found that neither species nor site were significantly different from one another. At first glance this is an odd result given that we can expect different years in Connecticut and the Townships to be characterized by different seed production schedules, granivore densities, etc—that is, by different fecundities (the product of seed production and survivorship). But consider that there appears to be some upper limit on fecundity (Greene and Johnson, 1998) set by an upper limit on seed production. Further, while seed production or survivorship can of course approach 0, in practice no investigator would include in her or his study a species which had a year with very poor fecundity. Thus, reported STR values that theoretically could span many orders of magnitude tend to vary only by several fold.

Seedbeds

The seedbed distribution found across all sites was typical of what should be present after a selection cut in a hardwood forest. (I have no data from other studies to compare with mine.) Note that while leaf litter was the most common seedbed (as is true for intact forests: Greene and Johnson, 1998), there was a large increase in exposed mineral soil and humus which is normally only about 1% or less of the forest floor. This was of course due to the presence of skid paths. The presence of these seedbeds increased the overall density of the small-seeded species due to an increase in their survivorship on litter-free substrates. Interestingly, I could detect no similar increase in survivorship for

the small-seeded species on the rotted wood substrates. It may be that the canopy has been sufficiently opened that the (elevated) rotted wood now becomes too dry during the summer to permit good early survivorship.

CONCLUSIONS

In summary, the lognormal is a better predictor of tree seedling recruitment than the Weibull. That being said, problems still exist with this modelling approach. The lognormal shape parameter tended to be far lower (on average) than expected by Greene et al (2004). The median distance (the location parameter) showed no species effect; that is, there was about as much variation within as among species. This was the first serious attempt at replication, and we could find no plausible default values. Why? I see two possibilities.

First, the sites are sufficiently different in factors such as mean wind speed at the time of the bulk of the abscission events, mean granivore density, mean wind direction, that site differences swamp the species differences. There are two main reasons to argue against this supposition. One reason is that the individual transects at each site (not shown in the preceding section) show about as much variation in parameter values as do the sites themselves. A second reason is that plausible site differences (e.g. granivore densities; wind regime) should not be linked to differences in favorability or to α . Yet these latter two parameters are just as variable among sites as the others.

I think a better explanation for the variation I have seen among sites is that the inverse modelling is introducing problems. One problem was discussed by Greene et al

(2004) where they argued that collisions of seeds with conspecific trunks can be interpreted by the algorithm as evidence for very short distance dispersal.

But there is another problem with inverse modelling, first touched upon by Calogeropoulos *et al.* (2003). They showed that while tree diameter may well be our single best predictor of seed production, it is nonetheless a poor predictor with an r^2 usually between 0.05 and 0.4 (except when trees are being lumped into diameter categories). As an example of the problems that can arise, picture a stand with one or two adjacent cherries producing almost all the seeds, a lognormal distribution of dispersed seed with a peak at (say) 15 m, and a clump of equal-sized trees at about 15 m from the seed-producers. The program would have to assume these similar-sized trees produced similar numbers of seeds and would interpret the dispersal curve as being rather poor with a peak close to the base of the typical cherry tree. Now at a second transect nearby, perhaps the two tallest trees produce 99% of the seeds. Now perhaps α is suitably increased so that production by smaller cherries around the transect is, effectively, ignored, and the program gets the dispersal parameters values more or less “right”. But of course those values are far different than we found for the first transect.

In summary, it may be that inverse modelling is not a “powerful” (Clark *et al.*, 1999) tool for disentangling parameter values when we have overlapping seed or seedling curves, but rather a very problematic and misleading approach. If so, the only alternatives for recruitment subroutine parameterization would be the very tedious and expensive approach of using molecular markers or using first principles arguments as advocated by Greene *et al.* (2004).

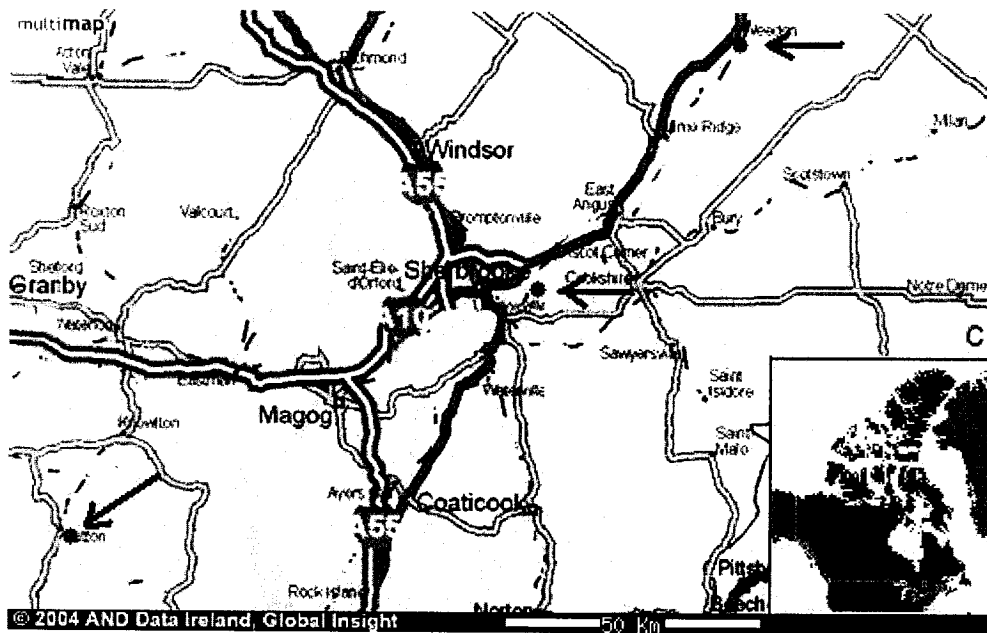


Figure 1: Map of the area surrounding the study sites. The three sites are indicated by a dot with an arrow pointing to each. Inset: map of Canada indicating location of the larger map

Recruitment subroutine

10 transects (50 m each) – 3 Stoke CJ2001, 3 Sutton CJ2001, 2 Sutton CJ2002,
2 Weedon CJT2001
1.5 ha of forest mapped / transect

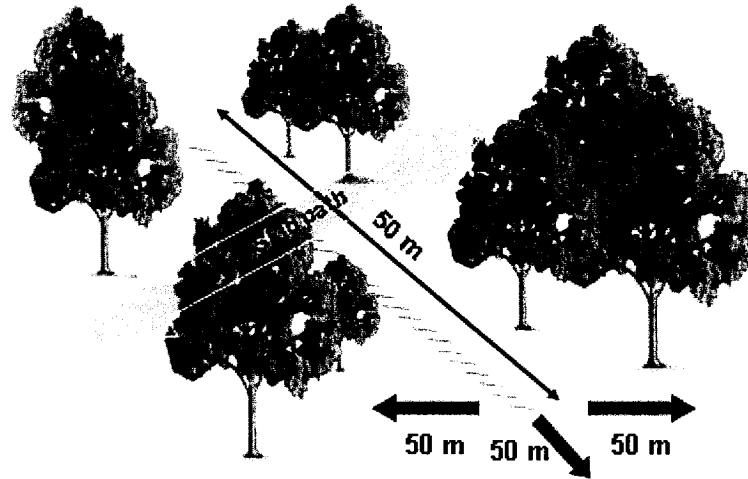


Figure 2: Diagram of transect set-up

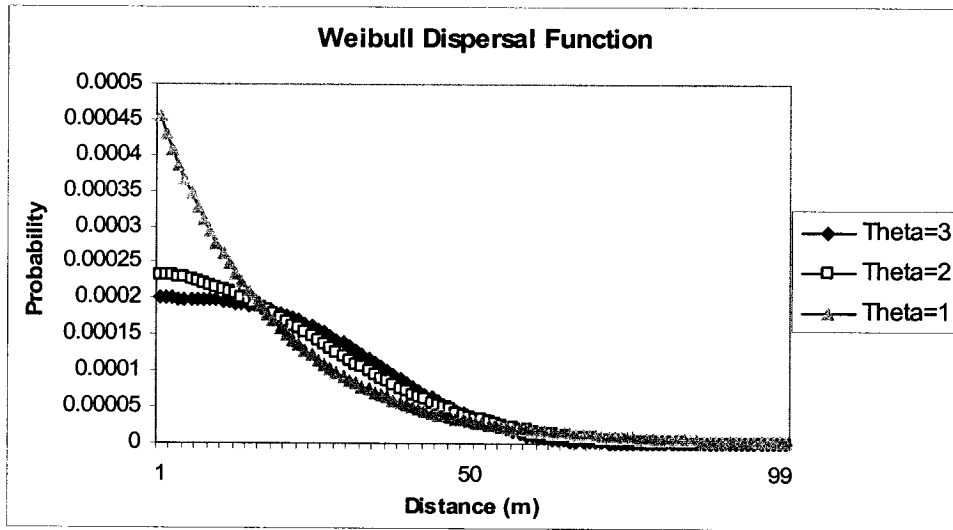


Figure 3a): Behavior of the Weibull dispersal curve given various values of θ

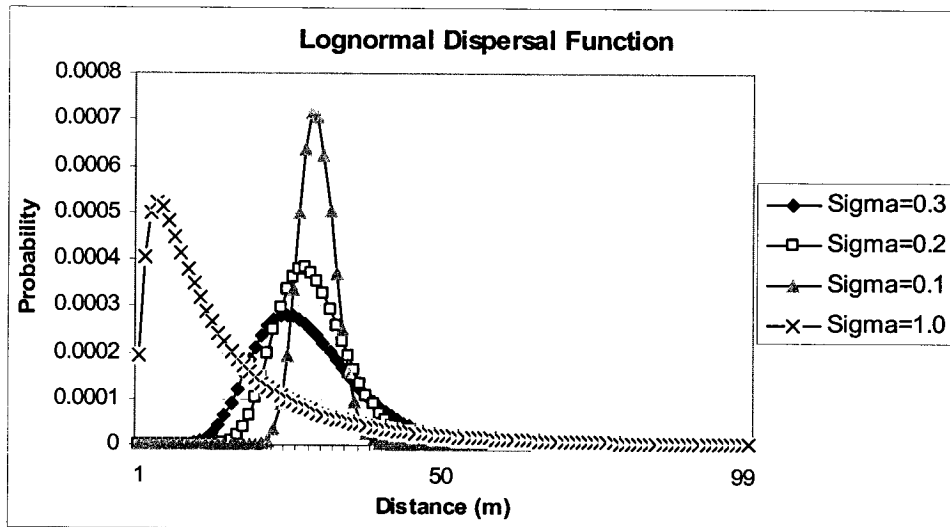


Figure 3b): Behavior of the lognormal dispersal curve given various values of σ

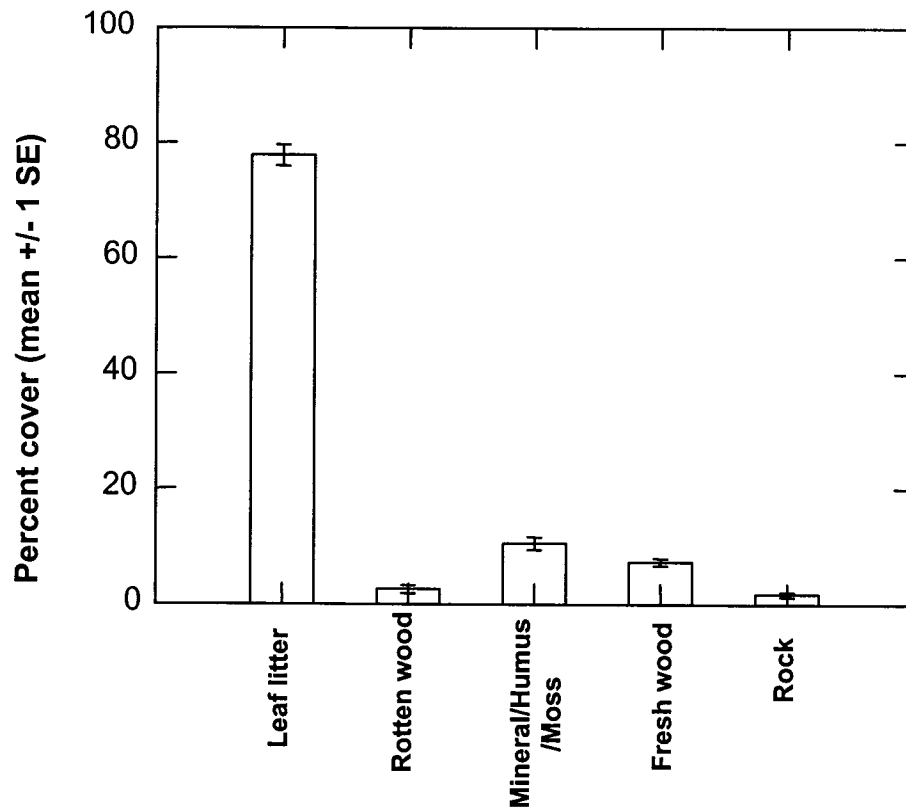


Figure 4: Proportion of seedbeds present averaged across all ten sites \pm 1 S.E.

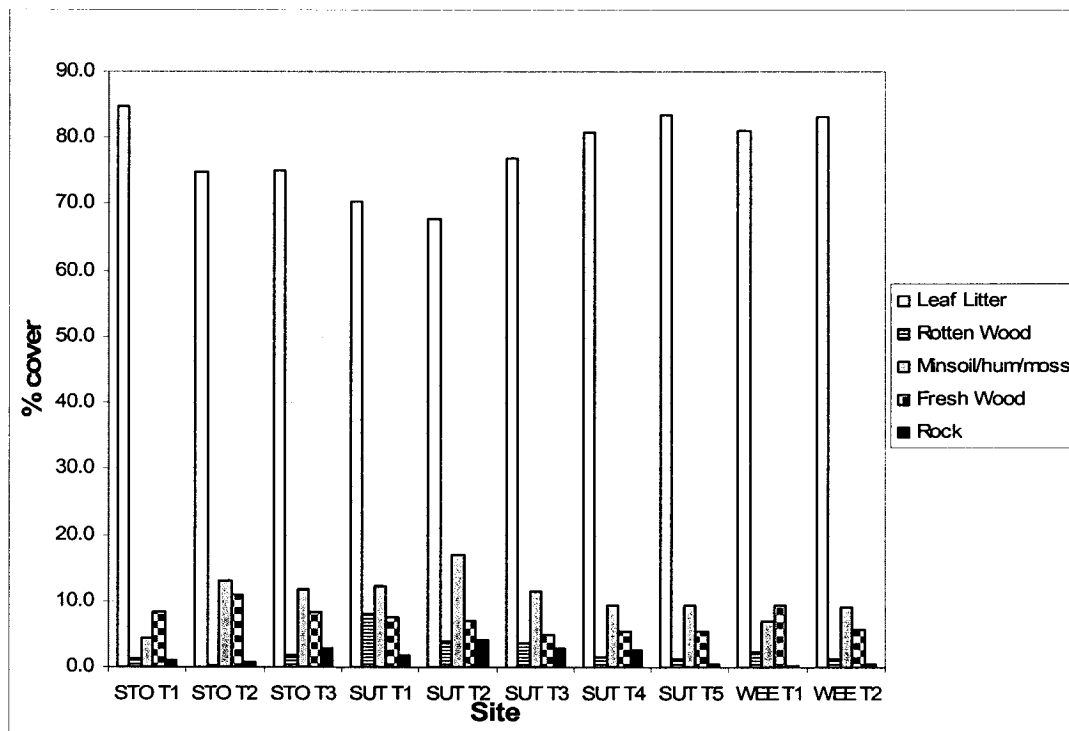


Figure 5: Seedbed distribution for each of the ten transects studied.
 STO: Stoke; SUT: Sutton; WEE: Weedon.
 Note: SUT T1, T2, T3 were studied in 2002 and SUT T4, T5 were studied in 2003

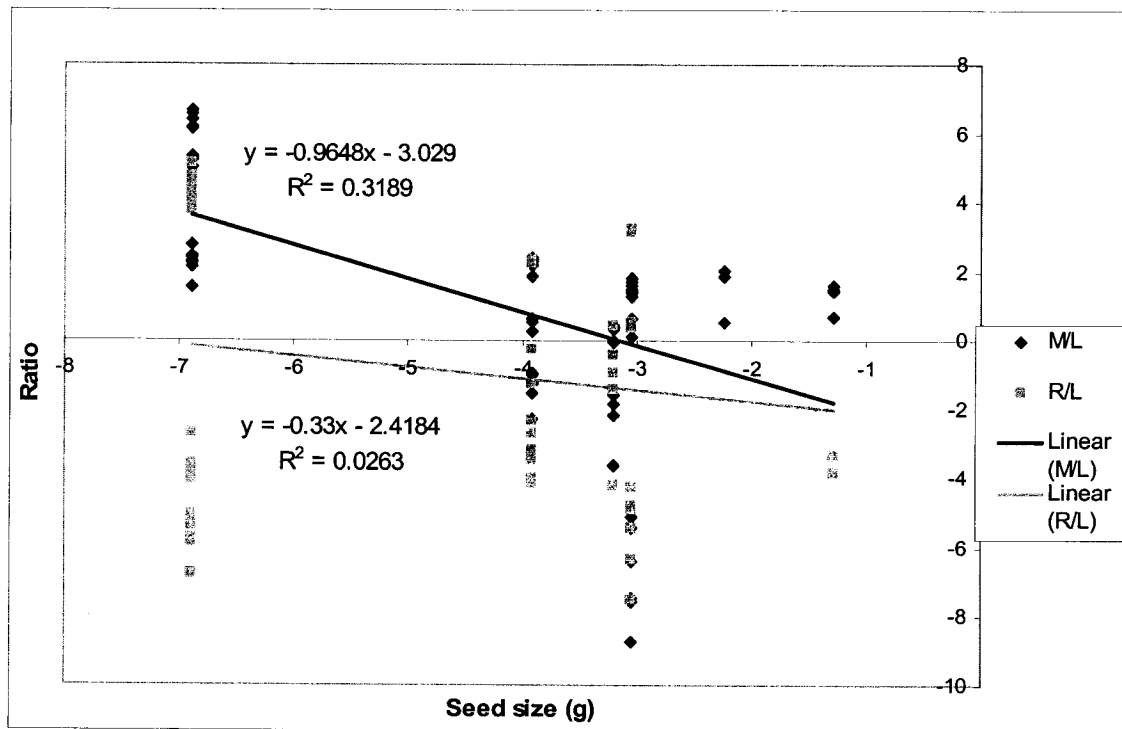


Figure 6: Seedbed favorability (generated by the recruitment subroutine) ratios as a function of seed size. M = mineral soil/humus/thin moss substrates, R = rotten wood, L = leaf litter

Table 1: Site characteristics

Note: SC: single-tree selection cut; GSC: group selection cut; BA: Basal area; AB: American beech; BC: black cherry; RM: red maple; StM: striped maple; SM: sugar maple; WA: white ash; YB: yellow birch, N/A: no potential for recruits – species not present at site.

(*) : for trees with DBH > 8 cm; > 5cm for striped maple

Stand	Type and year of cut	Sampling Year	Exposure (°)	BA * (m2/ha)	Density * (stems/ha)	Species composition (% BA per species)										# of potential parent trees										# of recruits									
						AB	BC	RM	StM	SM	WA	YB	AB	BC	RM	StM	SM	WA	YB	AB	BC	RM	StM	SM	WA	YB	AB	BC	RM	StM	SM	WA	YB		
STO1	SC Nov-Dec 2000	2002	92	13.1	441	24.4	0.0	29.7	1.7	22.1	0.0	22.1	154	0	110	67	165	0	166	0	N/A	120	11	12	N/A	52									
STO2	SC Nov-Dec 2000	2002	222	12.0	393	25.4	0.6	8.8	1.4	35.3	0.0	28.5	168	1	38	58	168	0	157	0	0	53	6	0	N/A	115									
STO3	SC Nov-Dec 2000	2002	216	13.5	377	24.2	0.2	2.5	0.5	55.5	0.7	16.3	170	1	14	22	234	2	122	1	3	35	1	2	0	106									
SUT1	SC Jul-Sep 2001	2002	100	19.0	421	11.2	2.9	0.0	0.0	70.6	3.9	11.4	89	12	0	1	422	25	83	7	23	N/A	9	174	6	11									
SUT2	SC Jul-Sep 2001	2002	219	20.9	429	14.9	0.0	1.3	0.1	68.9	5.2	9.7	164	0	5	9	369	33	63	1	N/A	4	7	16	26	42									
SUT3	SC Jul-Sep 2001	2002	136	20.0	340	14.6	0.6	0.0	0.0	66.2	2.1	16.5	85	2	1	1	314	14	93	6	1	0	8	225	30	86									
SUT4	SC Aug-Oct 2002	2003	42	22.4	333	10.0	1.4	0.0	0.0	72.6	9.0	7.0	80	7	0	0	344	30	39	47	1	N/A	N/A	26	79	494									
SUT5	SC Aug-Oct 2002	2003	353	22.7	428	14.0	1.4	0.2	0.0	63.1	11.2	10.2	173	3	1	1	348	49	67	10	23	0	7	2	13	469									
WEE1	GSC Aug-Sep 2001	2003	140	15.9	553	26.4	0.4	0.6	2.6	53.3	0.0	16.7	117	2	5	167	266	0	272	25	0	1	110	121	N/A	575									
WEE2	GSC Aug-Sep 2001	2003	170	17.0	467	20.2	0.1	1.0	1.4	66.7	0.9	9.7	85	2	4	97	336	4	173	3	0	4	80	155	3	184									

Table 2: Summary of values obtained from the parameter estimator

Note: SC: single-tree selection cut (up to 35% of basal area removed by removing single trees); GSC: group selection cut (up to 35% of basal area removed by removing both single trees and small groups of trees; $D/x_{0.5}$: location parameter, D for Weibull, $x_{0.5}$ for lognormal; θ/σ : shape parameter, θ for Weibull, σ for lognormal. A normalizer is not required for the lognormal function.

a) All sites

Species	Function	Treatment	# Parents	# Seedlings	Likelihood	Slope	MDD	Normalizer	STR	Alpha	$D/x_{0.5}$	θ/σ
Beech	Weibull	All vary	624	100	-246.53	1.23	7.48	233.25	119.62	3.35	99.30	2.13
	lognormal	All vary	624	100	-246.09	1.20	8.29		223.90	3.55	4.01	0.69
Black Cherry	Weibull	All vary	22	51	-133.93	0.99	46.16	4225.25	745.71	1.77	222.09	1.13
	lognormal	All vary	22	51	-128.27	1.03	110.15		1975.61	0.72	7.84	2.84
Red Maple	Weibull	All vary	120	217	-317.50	0.89	127.60	60820.58	98351.47	0.05	7.82	1.45
	lognormal	All vary	120	217	-301.99	0.89	58.30		75502.63	0.02	56.24	0.15
Striped Maple	Weibull	All vary	244	239	-447.90	1.08	55.14	7111.86	68912.55	0.01	98.14	1.25
	lognormal	All vary	244	239	-443.97	1.11	44.40		26439.24	0.10	27.27	0.57
Sugar Maple	Weibull	All vary	1340	733	-1117.19	1.03	7.13	339.34	725.31	3.12	0.00	8.58
	lognormal	All vary	1340	733	-1135.87	1.01	8.04		288.78	2.95	4.67	0.60
White Ash	Weibull	All vary	88	157	-288.58	0.96	32.23	6481.50	4247.67	5.10	0.00	5.21
	lognormal	All vary	88	157	-276.53	0.93	32.77		945.91	5.65	29.71	0.26
Yellow Birch	Weibull	All vary	598	2134	-2607.22	0.97	101.07	18116.98	16346.12	6.30	244.37	0.94
	lognormal	All vary	598	2134	-2661.79	0.78	38.89		10248.54	1.30	38.29	0.10

Table 2b): Stoke SC01

Species	Function	Treatment	# Parents	# Seedlings	Likelihood	Slope	MDD	Normalizer	STR	α	$D/X_{0.5}$	θ/c
Beech	Weibull	All vary	170	1								
		$\alpha=2$	170	1								
		$\alpha=2, \theta=2$	170	1								
		$\alpha=2, \theta=3$	170	1								
		All vary	170	1								
Black Cherry	lognormal	$\alpha=2$	170	1								
		All vary	1	3								
		$\alpha=2$	1	3								
		$\alpha=2, \theta=2$	1	3								
		$\alpha=2, \theta=3$	1	3								
Red Maple	Weibull	All vary	110	208								
		$\alpha=2$	110	208	-270.45	0.85	93.72	26947.06	99556.06	0.01	13.98	1.48
		$\alpha=2, \theta=2$	110	208	-280.86	0.81	112.70	41641.89	95147.85	2.00	11.85	1.44
		$\alpha=2, \theta=3$	110	208	-279.48	0.82	97.95	39039.30	99331.33	2.00	0.80	2.00
		All vary	110	208	-278.52	0.83	81.31	34375.78	99994.40	2.00	0.01	3.00
Striped Maple	lognormal	All vary	110	208	-259.61	0.88	55.95		55536.19	0.00	54.27	0.14
		$\alpha=2$	110	208	-273.62	0.87	61.69		97704.78	2.00	60.20	0.13
		All vary	67	18	-52.21	1.25	19.39	1017.83	39310.04	0.58	211.40	1.39
		$\alpha=2$	67	18	-53.35	1.24	13.85	638.68	98744.21	2.00	133.50	1.66
		$\alpha=2, \theta=2$	67	18	-53.34	1.17	13.75	753.75	98660.52	2.00	41.68	2.00
Sugar Maple	lognormal	$\alpha=2, \theta=3$	67	18	-53.50	1.23	14.36	1070.68	99813.49	2.00	1.36	3.00
		All vary	67	18	-51.60	1.00	20.09		81782.26	1.40	19.79	0.09
		$\alpha=2$	67	18	-52.83	1.07	15.64		92202.52	2.00	8.35	0.65
		All vary	234	14	-41.87	0.96	4.99	142.75	11.49	0.02	3.90	3.99
		$\alpha=2$	234	14	-48.49	0.86	9.87	538.53	23.83	2.00	1.05	3.48
White Ash	lognormal	$\alpha=2, \theta=2$	234	14	-48.54	0.84	10.15	410.12	22.31	2.00	76.60	2.00
		$\alpha=2, \theta=3$	234	14	-48.49	0.85	9.01	420.35	20.51	2.00	5.54	3.00
		All vary	234	14	-39.86	1.14	4.95		17.12	0.02	4.44	0.25
		$\alpha=2$	234	14	-44.40	0.79	85.04		164.99	2.00	84.95	0.01
		All vary	2	0								
Yellow Birch	Weibull	$\alpha=2$	2	0								
		$\alpha=2, \theta=2$	2	0								
		$\alpha=2, \theta=3$	2	0								
		All vary	2	0								
		$\alpha=2$	2	0								
Yellow Birch	lognormal	All vary	166	273	-408.88	0.74	25.92	4110.71	1092.22	0.01	0.00	4.79
		$\alpha=2$	166	273	-414.41	0.72	>50000	193652.13	34649.08	2.00	136.58	0.00
		$\alpha=2, \theta=2$	166	273	-416.24	0.72	309.64	153668.34	27225.47	2.00	0.08	2.00
		$\alpha=2, \theta=3$	166	273	-414.41	0.71	413.66	189561.08	34951.43	2.00	0.00	3.00
		All vary	166	273	-338.53	0.87	32.71		989.65	0.01	32.55	0.01
		$\alpha=2$	166	273	-415.14	0.72	93.74		6891.63	2.00	50.14	0.75

Table 2c): Sutton SC01

Species	Function	Treatment	# Parents	# Seedlings	Likelihood	Slope	MDD	Normalizer	STR	α	D/K _{0.5}	θ/α
Beech	Weibull	All vary	164	14	-43.43	0.87	5.85	173.81	98.69	2.65	24.28	2.93
		$\alpha=2$	164	14	-43.54	0.96	6.13	227.68	54.85	2.00	0.28	4.76
		$\alpha=2, \theta=2$	164	14	-44.09	0.90	6.01	142.31	60.30	2.00	220.78	2.00
		$\alpha=2, \theta=3$	164	14	-43.82	0.89	5.85	175.99	75.30	2.00	20.46	3.00
Black Cherry	lognormal	All vary	164	14	-42.48	0.91	102.13		2096.03	2.88	100.12	0.09
		$\alpha=2$	164	14	-43.03	0.89	106.02		5329.92	2.00	103.20	0.10
		All vary	12	24	-48.10	0.98	25.52	1542.76	391.69	5.97	244.82	1.27
		$\alpha=2$	12	24	-48.83	0.97	27.48	2910.53	895.42	2.00	14.57	1.92
	lognormal	$\alpha=2, \theta=2$	12	24	-48.82	0.94	27.94	3120.62	647.73	2.00	10.07	2.00
		$\alpha=2, \theta=3$	12	24	-48.74	0.95	28.77	4301.95	644.74	2.00	0.17	3.00
		All vary	12	24	-47.98	0.96	36.34		215.53	7.46	32.29	0.28
		$\alpha=2$	12	24	-48.48	0.95	35.98		819.11	2.00	33.52	0.22
Red Maple	Weibull	All vary	5	4								
		$\alpha=2$	5	4								
		$\alpha=2, \theta=2$	5	4								
		$\alpha=2, \theta=3$	5	4								
	lognormal	All vary	5	4								
		$\alpha=2$	5	4								
		All vary	9	24	-81.97	0.52	>50000	194028.49	61403.41	0.00	87.62	0.06
		$\alpha=2$	9	24	-90.11	0.47	96.15	50479.61	96539.37	2.00	0.00	3.35
Striped Maple	lognormal	$\alpha=2, \theta=2$	9	24	-90.76	0.49	123.90	68227.57	99533.54	2.00	0.43	2.00
		$\alpha=2, \theta=3$	9	24	-90.13	0.50	104.98	57514.67	99828.11	2.00	0.00	3.00
		All vary	9	24	-80.43	0.55	2107.23		94942.69	0.05	2302.61	1.53
		$\alpha=2$	9	24	-90.45	0.51	186.39		99249.25	2.00	114.97	0.98
Sugar Maple	Weibull	All vary	422	415	-529.51	1.05	9.88	588.43	508.17	3.18	0.02	4.88
		$\alpha=2$	422	415	-532.77	1.07	9.18	546.35	356.99	2.00	0.00	6.86
		$\alpha=2, \theta=2$	422	415	-535.87	1.07	10.30	422.13	513.00	2.00	74.43	2.00
		$\alpha=2, \theta=3$	422	415	-534.45	1.07	9.98	516.32	597.40	2.00	4.07	3.00
	lognormal	All vary	422	415	-508.38	1.09	10.99		266.42	4.26	10.29	0.21
		$\alpha=2$	422	415	-522.04	1.11	11.06		367.40	2.00	10.69	0.14
		All vary	33	62	-128.50	0.94	104.80	29290.34	2728.06	6.00	41.72	1.24
		$\alpha=2$	33	62	-132.60	0.89	31.09	5849.27	922.27	2.00	0.00	4.58
White Ash	lognormal	$\alpha=2, \theta=2$	33	62	-133.81	0.88	36.19	5832.99	987.98	2.00	5.39	2.00
		$\alpha=2, \theta=3$	33	62	-132.97	0.88	33.39	5796.75	3763.26	2.00	0.11	3.00
		All vary	33	62	-118.15	1.04	47.29		531.76	8.93	38.80	0.36
		$\alpha=2$	33	62	-129.84	0.87	32.59		3749.91	2.00	29.59	0.25
Yellow Birch	Weibull	All vary	93	139	-215.10	1.01	53.07	15435.51	1775.12	5.66	0.00	3.38
		$\alpha=2$	93	139	-223.96	1.00	56.41	16482.76	2419.86	2.00	0.02	2.98
		$\alpha=2, \theta=2$	93	139	-226.83	0.96	90.47	32995.69	8222.23	2.00	0.95	2.00
		$\alpha=2, \theta=3$	93	139	-226.15	0.97	63.82	21177.88	3032.35	2.00	0.02	3.00
	lognormal	All vary	93	139	-188.77	0.87	55.26		885.11	7.75	54.44	0.10
		$\alpha=2$	93	139	-197.09	1.04	62.21		2719.95	2.00	62.12	0.02

Table 2d): Sutton SC02

Species	Function	Treatment	# Parents	# Seedlings	Likelihood	Slope	MDD	Normalizer	STR	α	$D/K_{0.5}$	θ/g
Beech	Weibull	All vary	173	57	-93.46	1.06	8.98	349.46	218.22	3.15	49.23	2.24
		$\alpha=2$	173	57	-98.26	1.16	12.47	637.92	509.94	2.00	40.22	2.07
		$\alpha=2, \theta=2$	173	57	-98.24	1.15	12.69	642.23	525.63	2.00	48.92	2.00
		$\alpha=2, \theta=3$	173	57	-98.41	1.16	11.99	746.05	744.96	2.00	2.34	3.00
Black Cherry	Weibull	All vary	173	57	-94.38	1.00	21.39		480.65	4.98	2.20	0.96
		$\alpha=2$	173	57	-98.17	1.14	12.30		388.88	2.00	6.58	0.50
		All vary	7	24	-52.61	0.93	11.64	421.76	62.08	5.14	243.40	1.56
		$\alpha=2$	7	24	-53.33	0.95	9.50	299.69	178.95	2.00	249.60	1.66
	lognormal	$\alpha=2, \theta=2$	7	24	-54.05	0.93	9.32	345.29	389.13	2.00	90.99	2.00
		$\alpha=2, \theta=3$	7	24	-55.58	0.91	10.07	525.06	176.26	2.00	3.97	3.00
		All vary	7	24	-46.15	1.06	3.35		168.34	5.43	0.26	2.32
		$\alpha=2$	7	24	-47.88	1.09	1.80		997.81	2.00	0.12	2.64
Red Maple	Weibull	All vary	0	0								
		$\alpha=2$	0	0								
		$\alpha=2, \theta=2$	0	0								
		$\alpha=2, \theta=3$	0	0								
	lognormal	All vary	0	0								
		$\alpha=2$	0	0								
		All vary	10	7								
		$\alpha=2$	1	7								
Striped Maple	Weibull	$\alpha=2, \theta=2$	1	7								
		$\alpha=2, \theta=3$	1	7								
		All vary	1	7								
		$\alpha=2$	1	7								
Sugar Maple	Weibull	All vary	348	28	-47.00	1.09	8.41	412.10	3.30	8.46	0.41	4.05
		$\alpha=2$	348	28	-61.56	0.91	6.38	245.99	407.73	2.00	0.27	4.70
		$\alpha=2, \theta=2$	348	28	-63.14	0.93	7.33	212.68	305.72	2.00	147.73	2.00
		$\alpha=2, \theta=3$	348	28	-62.24	0.94	6.70	231.10	398.57	2.00	13.60	3.00
	lognormal	All vary	348	28	-45.76	1.13	7.69		8.86	7.71	7.03	0.24
		$\alpha=2$	348	28	-54.80	1.02	66.80		520.02	2.00	66.19	0.00
		All vary	49	92	-123.44	0.96	>50000	195997.03	582.04	11.08	2.72	0.37
		$\alpha=2$	49	92	-147.04	1.03	28.34	5059.37	1714.89	2.00	0.00	5.47
White Ash	Weibull	$\alpha=2, \theta=2$	49	92	-150.01	1.00	28.01	3137.25	1626.00	2.00	10.01	2.00
		$\alpha=2, \theta=3$	49	92	-148.30	1.01	26.81	3735.91	1392.45	2.00	0.21	3.00
		All vary	49	92	-118.66	0.84	479.57		1487.41	10.33	379.68	0.88
		$\alpha=2$	49	92	-139.42	1.01	46.52		1609.43	2.00	46.39	0.03
Yellow Birch	Weibull	All vary	67	963	-339.11	1.17	351.08	77832.05	69703.63	8.11	66.60	0.98
		$\alpha=2$	67	963	-335.79	1.18	25.79	4209.03	40386.78	2.00	0.00	5.59
		$\alpha=2, \theta=2$	67	963	-346.41	1.17	28.21	3181.43	62869.29	2.00	9.87	2.00
		$\alpha=2, \theta=3$	67	963	-340.61	1.17	25.74	3442.11	34979.53	2.00	0.24	3.00
	lognormal	All vary	67	963	-314.69	1.03	21.99		49520.47	3.40	18.71	0.33
		$\alpha=2$	67	963	-317.70	1.10	23.82		33467.54	2.00	19.89	0.35

Table 2e): Weedon GSC01

Species	Function	Treatment	# Parents	# Seedlings	Likelihood	Slope	MDD	Normalizer	STR	α	$D/\lambda_{0.5}$	θ/α
Beech	Weibull	All vary	117	28	-51.79	1.00	6.32	180.55	22.30	5.96	73.57	2.39
		$\alpha=2$	117	28	-56.85	1.13	7.16	290.68	107.89	2.00	1.55	3.78
		$\alpha=2;\theta=2$	117	28	-57.22	1.08	7.24	207.41	184.03	2.00	151.48	2.00
	lognormal	$\alpha=2;\theta=3$	117	28	-56.88	1.08	7.14	263.02	259.74	2.00	11.20	3.00
		All vary	117	28	-53.44	1.05	82.43		655.44	5.98	81.67	0.08
Black Cherry	Weibull	$\alpha=2$	117	28	-55.70	0.87	90.46		1389.60	2.00	90.16	0.05
		All vary	2	0								
		$\alpha=2$	2	0								
	lognormal	$\alpha=2;\theta=2$	2	0								
		$\alpha=2;\theta=3$	2	0								
Red Maple	Weibull	All vary	2	0								
		$\alpha=2$	2	0								
		$\alpha=2$	5	5								
	lognormal	$\alpha=2;\theta=2$	5	5								
		$\alpha=2;\theta=3$	5	5								
Striped Maple	Weibull	All vary	167	190	-200.36	0.99	19.79	2384.97	94321.83	4.64	0.00	4.89
		$\alpha=2$	167	190	-207.40	1.04	22.48	3224.00	5154.79	2.00	0.00	5.88
		$\alpha=2;\theta=2$	167	190	-213.61	1.04	24.63	2425.12	8716.18	2.00	12.95	2.00
	lognormal	$\alpha=2;\theta=3$	167	190	-210.72	1.05	23.66	2908.80	6761.12	2.00	0.30	3.00
		All vary	167	190	-189.00	0.90	17.57		96043.67	4.64	17.11	0.13
Sugar Maple	Weibull	$\alpha=2$	167	190	-197.10	1.02	25.09		8098.17	2.00	23.56	0.20
		All vary	336	276	-267.63	0.99	>50000	189649.92	4881.60	5.34	75.94	0.30
		$\alpha=2$	336	276	-268.70	0.96	>50000	196251.74	25058.32	2.00	2.79	0.12
	lognormal	$\alpha=2;\theta=2$	336	276	-268.69	0.97	1568.14	194402.77	12199.45	2.00	0.00	2.00
		$\alpha=2;\theta=3$	336	276	-250.38	0.97	6.10	191.24	4306.36	2.00	18.06	3.00
White Ash	Weibull	All vary	336	276	-228.80	0.97	9.17		553.29	3.76	2.26	0.96
		$\alpha=2$	336	276	-247.36	0.99	7.49		2065.73	2.00	2.63	0.83
		All vary	4	3								
	lognormal	$\alpha=2$	4	3								
		$\alpha=2;\theta=2$	4	3								
Yellow Birch	Weibull	$\alpha=2;\theta=3$	4	3								
		All vary	4	3								
		$\alpha=2$	4	3								
	lognormal	$\alpha=2$	272	759	-400.03	0.92	18.23	1290.99	54522.70	3.78	29.77	1.94
		$\alpha=2$	272	759	-464.10	1.13	24.38	3672.04	56074.64	2.00	0.00	5.00

Table 3: Results of a regression analysis between predicted and observed seedling recruits. * : slope is significantly different from 1.0; ** : intercept is significantly different from 0.0; shading: regression is not significant

a): Stoke SC01

	R ²	Slope	Intercept	F	p
Stoke					
Species 3 - ERR					
Weibull All vary	0.1308	*0.68	0.41	21.91	0.00
Weibull Alpha=2	0.1247	*0.60	**0.53	20.76	0.00
Weibull Alpha=2, Theta=2	0.1264	*0.62	**0.52	21.08	0.00
Weibull Alpha=2, Theta=3	0.1281	*0.63	**0.51	21.40	0.00
Lognormal All vary	0.1534	0.73	0.36	26.43	0.00
Lognormal Alpha=2	0.1494	*0.70	0.41	25.60	0.00
Species 4 - ERP					
Weibull All vary	0.1516	*1.69	-0.09	26.42	0.00
Weibull Alpha=2	0.0983	0.50	0.06	0.73	0.39
Weibull Alpha=2, Theta=2	0.0974	*0.03	**0.16	0.02	0.89
Weibull Alpha=2, Theta=3	0.1011	1.35	-0.03	16.56	0.00
Lognormal All vary	0.1343	*2.15	**0.10	45.84	0.00
Lognormal Alpha=2	0.0888	1.11	-0.01	14.35	0.00
Species 5 - ERS					
Weibull All vary	0.0517	0.95	0.00	8.00	0.01
Weibull Alpha=2	0.0053	0.47	0.05	0.74	0.39
Weibull Alpha=2, Theta=2	0.0046	0.43	0.05	0.64	0.42
Weibull Alpha=2, Theta=3	0.0049	0.43	0.05	0.69	0.41
Lognormal All vary	0.0915	1.23	-0.02	14.84	0.00
Lognormal Alpha=2	0.0239	0.59	0.04	3.57	0.06
Species 7 - BOJ					
Weibull All vary	0.0685	*0.51	**0.89	10.71	0.00
Weibull Alpha=2	0.0654	*0.49	**0.93	10.20	0.00
Weibull Alpha=2, Theta=2	0.0639	*0.48	**0.94	9.93	0.00
Weibull Alpha=2, Theta=3	0.0654	*0.48	**0.94	10.19	0.00
Lognormal All vary	0.1728	0.77	0.42	30.68	0.00
Lognormal Alpha=2	0.0641	*0.49	**0.93	9.97	0.00

Table 3b): Sutton SC01

	R ²	Slope	Intercept	F	p
SutCJ01					
Species 1 - HEG					
Weibull All vary	0.0266	0.65	0.03	3.98	0.05
Weibull Alpha=2	0.0317	0.84	0.02	4.78	0.03
Weibull Alpha=2, Theta=2	0.0228	0.67	0.03	3.39	0.07
Weibull Alpha=2, Theta=3	0.0259	0.69	0.03	3.87	0.05
Lognormal All vary	0.0588	0.78	0.02	9.22	0.00
Lognormal Alpha=2	0.0577	0.79	0.02	9.03	0.00
Species 2 - CET					
Weibull All vary	0.1929	0.94	0.02	23.19	0.00
Weibull Alpha=2	0.1756	0.93	0.02	20.65	0.00
Weibull Alpha=2, Theta=2	0.1752	0.90	0.02	20.59	0.00
Weibull Alpha=2, Theta=3	0.1775	0.90	0.03	20.92	0.00
Lognormal All vary	0.1937	0.90	0.03	23.32	0.00
Lognormal Alpha=2	0.1848	0.89	0.03	22.00	0.00
Species 4 - ERP					
Weibull All vary	0.0038	*0.13	**0.14	0.52	0.47
Weibull Alpha=2	0.0007	*0.05	**0.15	0.09	0.77
Weibull Alpha=2, Theta=2	0.0003	*0.03	**0.15	0.03	0.87
Weibull Alpha=2, Theta=3	0.0010	*0.07	**0.15	0.13	0.72
Lognormal All vary	0.0067	*0.18	**0.13	0.96	0.33
Lognormal Alpha=2	0.0000	*0.01	**0.16	0.00	0.95
Species 5 - ERS					
Weibull All vary	0.1114	1.26	-0.75	18.44	0.00
Weibull Alpha=2	0.1088	1.35	-0.97	17.97	0.00
Weibull Alpha=2, Theta=2	0.1045	1.42	-1.17	17.17	0.00
Weibull Alpha=2, Theta=3	0.1080	1.43	-1.22	17.83	0.00
Lognormal All vary	0.1639	1.30	-0.78	28.95	0.00
Lognormal Alpha=2	0.1483				
Species 6 - FRA					
Weibull All vary	0.0574	0.77	0.10	8.79	0.00
Weibull Alpha=2	0.0252	0.51	0.20	3.63	0.06
Weibull Alpha=2, Theta=2	0.0213	0.49	0.21	3.02	0.08
Weibull Alpha=2, Theta=3	0.0249	0.52	0.20	3.58	0.06
Lognormal All vary	0.1485	1.13	-0.05	25.66	0.00
Lognormal Alpha=2	0.0361	0.55	0.18	5.35	0.02
Species 7 - BOJ					
Weibull All vary	0.2223	1.03	-0.02	42.36	0.00
Weibull Alpha=2	0.1580	0.99	0.01	27.73	0.00
Weibull Alpha=2, Theta=2	0.1429	0.92	0.07	24.64	0.00
Weibull Alpha=2, Theta=3	0.1466	0.94	0.05	25.39	0.00
Lognormal All vary	0.3280	0.81	0.17	72.46	0.00
Lognormal Alpha=2	0.2867	1.08	-0.07	59.63	0.00

Table 3c): Sutton SC01

	R ²	Slope	Intercept	F	p
SutCJ02					
Species 1 - HEG					
Weibull All vary	0.4121	1.19	-0.07	39.82	0.00
Weibull Alpha=2	0.3658	1.33	-0.18	57.38	0.00
Weibull Alpha=2, Theta=2	0.3656	1.31	-0.17	57.31	0.00
Weibull Alpha=2, Theta=3	0.3639	1.33	-0.18	56.90	0.00
Lognormal All vary	0.4022	1.01	-0.02	66.90	0.00
Lognormal Alpha=2	0.3782	1.29	-0.16	60.51	0.00
Species 2 - CET					
Weibull All vary	0.1044	0.89	0.02	11.55	0.00
Weibull Alpha=2	0.1139	0.90	0.02	12.75	0.00
Weibull Alpha=2, Theta=2	0.1035	0.87	0.03	11.43	0.00
Weibull Alpha=2, Theta=3	0.0795	0.83	0.04	8.53	0.00
Lognormal All vary	0.3694	1.09	-0.03	58.44	0.00
Lognormal Alpha=2	0.4273	1.12	-0.03	74.46	0.00
Species 5 - ERS					
Weibull All vary	0.5422	1.28	-0.10	81.33	0.00
Weibull Alpha=2	0.1202	0.82	0.05	13.44	0.00
Weibull Alpha=2, Theta=2	0.0999	0.84	0.04	10.88	0.00
Weibull Alpha=2, Theta=3	0.1137	0.87	0.03	12.60	0.00
Lognormal All vary	0.5591	1.19	-0.05	126.37	0.00
Lognormal Alpha=2	0.2448	1.01	0.00	32.14	0.00
Species 6 - FRA					
Weibull All vary	0.3429	0.92	0.08	51.86	0.00
Weibull Alpha=2	0.2034	1.09	-0.09	25.27	0.00
Weibull Alpha=2, Theta=2	0.1779	0.99	0.00	21.38	0.00
Weibull Alpha=2, Theta=3	0.1913	1.03	-0.03	23.38	0.00
Lognormal All vary	0.3518	*0.79	0.18	53.97	0.00
Lognormal Alpha=2	0.2271	1.03	-0.03	29.11	0.00
Species 7 - BOJ					
Weibull All vary	0.8112	*1.22	-2.11	429.04	0.00
Weibull Alpha=2	0.8269	*1.23	-2.15	477.12	0.00
Weibull Alpha=2, Theta=2	0.8217	*1.22	-2.09	460.24	0.00
Weibull Alpha=2, Theta=3	0.8249	*1.22	-2.06	470.59	0.00
Lognormal All vary	0.8056	1.04	-0.37	413.57	0.00
Lognormal Alpha=2	0.8256	*1.13	-1.25	472.72	0.00

Table 3d): Weedon GSC01

	R ²	Slope	Intercept	F	p
Weedon					
Species 1 - HEG					
Weibull All vary	0.2556	1.00	0.00	33.77	0.00
Weibull Alpha=2	0.1804	1.25	-0.06	21.60	0.00
Weibull Alpha=2, Theta=2	0.1739	1.18	-0.05	20.65	0.00
Weibull Alpha=2, Theta=3	0.1790	1.19	-0.05	21.40	0.00
Lognormal All vary	0.2352	1.10	-0.03	30.24	0.00
Lognormal Alpha=2	0.1281	0.77	0.07	14.37	0.00
Species 4 - ERP					
Weibull All vary	0.2140	0.98	0.03	26.31	0.00
Weibull Alpha=2	0.2079	1.25	-0.49	25.40	0.00
Weibull Alpha=2, Theta=2	0.1770	1.23	-0.44	20.71	0.00
Weibull Alpha=2, Theta=3	0.1907	1.25	-0.46	22.75	0.00
Lognormal All vary	0.2500	0.77	0.45	32.37	0.00
Lognormal Alpha=2	0.2342	1.07	-0.12	29.61	0.00
Species 5 - ERS					
Weibull All vary	0.1097	0.94	0.15	11.52	0.00
Weibull Alpha=2	0.0928	0.79	0.58	9.48	0.00
Weibull Alpha=2, Theta=2	0.0941	0.81	0.52	9.64	0.00
Weibull Alpha=2, Theta=3	0.1473	0.87	0.36	16.40	0.00
Lognormal All vary	0.2799	0.92	0.21	37.64	0.00
Lognormal Alpha=2	0.2006	0.96	0.11	24.07	0.00
Species 7 - BOJ					
Weibull All vary	0.8498	*0.91	0.66	559.28	0.00
Weibull Alpha=2	0.7110	*1.17	-1.31	243.19	0.00
Weibull Alpha=2, Theta=2	0.6569	1.14	-1.01	189.17	0.00
Weibull Alpha=2, Theta=3	0.6830	1.16	-1.15	212.91	0.00
Lognormal All vary	0.8556	0.94	0.48	585.60	0.00
Lognormal Alpha=2	0.8250	*1.19	-1.42	466.10	0.00

Table 4: Comparison of the log-likelihood values obtained from the parameter estimator using the Weibull and lognormal dispersal functions.

		Stoke		SutC-J01		SutC-J02		Weedon		Total		All sites pooled	
		Weibull	lognormal	Weibull	lognormal	Weibull	lognormal	Weibull	lognormal	Weibull	lognormal	Weibull	lognormal
All vary	# better	0	4	0	6	1	4	1	3	2	17	2	5
	# signif. better	0	2	0	3	0	3	0	3	0	11	2	4
alpha=2	# better	1	3	1	5	0	5	0	4	2	17	x	x
	# signif. better	0	2	0	2	0	4	0	3	0	11	x	x

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Appendix I:

a) θ values with confidence limits obtained using Weibull

All	lower	upper	Stoke	lower	upper	SutCJ01	lower	upper	SutCJ02	lower	upper	Weedon	lower	upper
Beech														
Alpha vary	2.1294	1.9910	2.2679	x	x	2.9282	2.4011	3.2942	2.2362	1.8337	2.3480	2.3896	2.0431	2.6405
Alpha = 2				x	x	4.7605	3.9988	5.3556	2.0707	1.8740	2.2778	3.7754	3.2846	4.1907
Black Cherry														
Alpha vary	1.1336	1.0712	1.1903	x	x	1.2872	1.0898	1.4065	1.5621	1.3981	1.7340	x	x	x
Alpha = 2				x	x	1.9174	1.6869	2.0995	1.6561	1.4822	1.8134	x	x	x
Red Maple														
Alpha vary	1.4529	1.4093	1.4892	1.4793	1.4349	1.5089	x	x	x	x	x	x	x	x
Alpha = 2				1.4408	1.4048	1.4696	x	x	x	x	x	x	x	x
Striped Maple														
Alpha vary	1.2545	1.2231	1.2921	1.3924	1.1000	1.6778	0.0607	0.7786	x	x	x	4.6943	4.4361	5.0229
Alpha = 2				1.6558	1.2501	1.9290	3.3451	3.4622	x	x	x	5.8766	5.6122	6.0236
Sugar Maple														
Alpha vary	8.5798	8.4082	8.7943	3.9869	2.8506	4.9238	4.8840	5.0061	4.0456	3.8029	4.8548	0.3007	0	0.6585
Alpha = 2				3.4846	2.7528	5.0003	6.6576	6.9572	4.7014	4.0902	5.1490	0.1151	0	1.2206
White Ash														
Alpha vary	5.2102	5.0539	5.3404	x	x	x	1.2406	1.1848	0.3727	0	1.3418	x	x	x
Alpha = 2				x	x	x	4.5780	4.2804	5.4662	5.2202	5.8488	x	x	x
Yellow Birch														
Alpha vary	0.9365	0.9272	0.9459	4.7876	4.5243	4.9551	3.3785	3.2603	0.9775	0.9580	0.9971	1.3375	1.9085	1.9666
Alpha = 2				0.0025	0	0.5483	2.9774	2.8732	5.5934	5.4536	5.7612	4.9974	4.9224	5.0223

b) σ values with confidence limits obtained using lognormal

All	lower	upper	Stoke	lower	upper	SutCJ01	lower	upper	SutCJ02	lower	upper	Weedon	lower	upper
Beech														
Alpha vary	0.6931	0.6272	0.7832	x	x	0.0891	0.0601	0.1501	0.9574	0.8665	1.0819	0.0782	0.0489	0.1255
Alpha = 2				x	x	0.1036	0.0694	0.1631	0.5008	0.3580	0.6460	0.0457	0.0320	0.0871
Black Cherry														
Alpha vary	2.8398	2.7120	3.0812	x	x	0.2804	0.1935	0.3995	2.3179	2.1673	2.4918	x	x	x
Alpha = 2				x	x	0.2172	0.1499	0.3638	2.6439	2.4853	2.8290	x	x	x
Red Maple														
Alpha vary	0.1545	0.1066	0.2047	0.1422	0.0981	0.2048	x	x	x	x	x	x	x	x
Alpha = 2				0.1276	0.0867	0.1933	x	x	x	x	x	x	x	x
Striped Maple														
Alpha vary	0.5716	0.5144	0.6287	0.0932	0.0671	0.1631	1.5329	2.3529	x	x	x	0.1286	0.0984	0.1807
Alpha = 2				0.6462	0.4652	0.9757	0.9835	1.5539	x	x	x	0.2035	0.1496	0.2686
Sugar Maple														
Alpha vary	0.5991	0.5631	0.6410	0.2517	0.1473	0.5047	0.2060	0.2493	0.2364	0.1678	0.3404	0.9616	0.8895	1.0241
Alpha = 2				0.0096	0.0052	0.0361	0.1405	0.1763	0.0016	0.0010	0.0026	0.8312	0.7647	0.9018
White Ash														
Alpha vary	0.2554	0.2056	0.3217	x	x	x	0.3630	0.2777	0.6838	0.6291	0.7385	x	x	x
Alpha = 2				x	x	x	0.2535	0.1724	0.0349	0.0263	0.0471	x	x	x
Yellow Birch														
Alpha vary	0.1008	0.0903	0.1099	0.0133	0.0111	0.0166	0.0990	0.0768	0.3278	0.2901	0.3672	0.4861	0.4618	0.5080
Alpha = 2				0.7475	0.7026	0.7981	0.0190	0.0149	0.3462	0.3047	0.3947	0.0459	0.0408	0.0525

= not significantly different from 1.0

Appendix II:

a) D values obtained using Weibull

	All sites	d/10000	Stoke	d/10000	SutCJ01	d/10000	SutCJ02	d/10000	Weedon	d/10000
Beech										
Alpha vary	99.3035	0.0099	x	x	24.2764	0.0024	49.2270	0.0049	73.5695	0.0074
Alpha = 2			x	x	0.2803	0.0000	40.2223	0.0040	1.5507	0.0002
Black Cherry										
Alpha vary	222.0886	0.0222	x	x	244.8244	0.0245	243.3954	0.0243	x	x
Alpha = 2			x	x	14.5744	0.0015	249.5976	0.0250	x	x
Red Maple										
Alpha vary	7.8241	0.0008	13.9803	0.0014	x	x	x	x	x	x
Alpha = 2			11.8505	0.0012	x	x	x	x	x	x
Striped Maple										
Alpha vary	98.1357	0.0098	211.3961	0.0211	87.6183	0.0088	x	x	0.0013	0.0000
Alpha = 2			133.5049	0.0134	0.0008	0.0000	x	x	0.0000	0.0000
Sugar Maple										
Alpha vary	0.0000	0.0000	3.9048	0.0004	0.0202	0.0000	0.4071	0.0000	75.9400	0.0076
Alpha = 2			1.0476	0.0001	0.0002	0.0000	0.2661	0.0000	2.7901	0.0003
White Ash										
Alpha vary	0.0000	0.0000	x	x	41.7237	0.0042	2.7228	0.0003	x	x
Alpha = 2			x	x	0.0002	0.0000	0.0000	0.0000	x	x
Yellow Birch										
Alpha vary	244.3689	0.0244	0.0003	0.0000	0.0048	0.0000	66.5881	0.0067	29.7688	0.0030
Alpha = 2			136.5777	0.0137	0.0249	0.0000	0.0000	0.0000	0.0002	0.0000

b) X_{0.5} values obtained using lognormal

	All Sites	Stoke	SutCJ01	SutCJ02	Weedon	St.Hilaire
Beech						
Alpha vary	4.0089	x	100.9157	5.4935	81.6705	
Alpha = 2		x	104.3172	8.4300	90.1590	
Black Cherry						
Alpha vary	7.8370	x	32.2886	0.2569	x	
Alpha = 2		x	33.5169	0.1198	x	
Red Maple						
Alpha vary	56.2422	54.2691	x	x	x	
Alpha = 2		60.1968	x	x	x	0.26
Striped Maple						
Alpha vary	27.2660	19.7927	2302.6098	x	17.1081	
Alpha = 2		8.3510	114.9663	x	23.5612	13.6
Sugar Maple						
Alpha vary	4.6698	4.4441	10.2855	7.0332	2.2633	
Alpha = 2		84.9472	10.6919	66.1934	2.6281	12.8
White Ash						
Alpha vary	29.7121	x	38.8029	379.6849	x	
Alpha = 2		x	29.5873	46.3940	x	
Yellow Birch						
Alpha vary	38.2870	32.5498	54.4384	18.7060	13.4279	
Alpha = 2		50.1367	62.1222	19.8895	25.4077	

Appendix III:

a) MDD values obtained using Weibull

	Stoke	SutCJ01	SutCJ02	Weedon	St.Hilaire	Ribbens
Beech						
α vary	x	5.849	8.984	6.32		x
$\alpha=2$	x	6.129	12.469	7.156		x
$\alpha=2, \theta=2$	x	6.006	12.69	7.235		x
$\alpha=2, \theta=3$	x	5.85	11.993	7.138		10.567
Black Cherry						
α vary	x	25.517	11.635			x
$\alpha=2$	x	27.481	9.502	x		x
$\alpha=2, \theta=2$	x	27.94	9.317	x		x
$\alpha=2, \theta=3$	x	28.769	10.067	x		8.038
Red Maple						
α vary	93.719	x	x	x	19	x
$\alpha=2$	112.702	x	x	x		x
$\alpha=2, \theta=2$	97.945	x	x	x		x
$\alpha=2, \theta=3$	81.306	x	x	x	24.7	9.525
Striped Maple						
α vary	19.392	>50000	x	19.793	43	x
$\alpha=2$	13.849	96.151	x	22.476		x
$\alpha=2, \theta=2$	13.745	123.896	x	24.633		x
$\alpha=2, \theta=3$	14.362	104.976	x	23.659	25.9	x
Sugar Maple						
α vary	4.987	9.88	8.413	>50000	14	x
$\alpha=2$	9.869	9.175	6.378	>50000		x
$\alpha=2, \theta=2$	10.15	10.297	7.325	1568.141		x
$\alpha=2, \theta=3$	9.012	9.983	6.695	6.095	13.9	8.150
White Ash						
α vary	x	104.804	>50000			x
$\alpha=2$	x	31.088	28.342	x		x
$\alpha=2, \theta=2$	x	38.193	28.014	x		x
$\alpha=2, \theta=3$	x	33.393	26.81	x		16.341
Yellow Birch						
α vary	25.919	53.069	351.0819	18.225		x
$\alpha=2$	>50000	56.406	25.794	24.375		x
$\alpha=2, \theta=2$	309.6353	90.473	28.211	22.968		x
$\alpha=2, \theta=3$	413.656	63.819	25.735	23.232		>66

b) MDD values obtained using lognormal

	Stoke	SutCJ01	SutCJ02	Weedon	St.Hilaire
Beech					
Alpha vary	x	102.131	21.387	82.433	
Alpha = 2	x	106.015	12.302	90.457	
Black Cherry					
Alpha vary	x	36.337	3.346745	x	
Alpha = 2	x	35.983	1.801831	x	
Red Maple					
Alpha vary	55.95	x	x	x	
Alpha = 2	61.693	x	x	x	
Striped Maple					
Alpha vary	20.087	173.05	x	17.567	
Alpha = 2	15.644	138.593	x	25.085	20.4
Sugar Maple					
Alpha vary	4.95	10.994	7.69	9.165	
Alpha = 2	85.037	11.057	66.8	7.49	14
White Ash					
Alpha vary	x	47.287	479.5699	x	
Alpha = 2	x	32.59	46.518	x	
Yellow Birch					
Alpha vary	32.706	55.257	21.99	19.154	
Alpha = 2	93.74	62.21	23.817	25.543	

Appendix IV:

a) α values with confidence limits obtained using Weibull

	All	lower	upper	Stoke	lower	upper	SutCJ01	lower	upper	SutCJ02	lower	upper	Weedon	lower	upper
Beech	3.3476	2.6111	4.1343	x	x	x	2.8543	1.2608	5.0565	3.1523	2.2696	5.9105	5.9609	4.8283	6.0205
Alpha vary	3.3476	2.6111	4.1343	x	x	x	2.8543	1.2608	5.0565	3.1523	2.2696	5.9105	5.9609	4.8283	6.0205
Black Cherry	1.7714	0.6731	2.5154	x	x	x	5.9695	3.8802	6.0292	5.1425	4.2169	5.8625	x	x	x
Alpha vary	1.7714	0.6731	2.5154	x	x	x	5.9695	3.8802	6.0292	5.1425	4.2169	5.8625	x	x	x
Red Maple	0.0466	0.0000	0.2972	0.0101	-0.0001	0.2745	x	x	x	x	x	x	x	x	x
Alpha vary	0.0466	0.0000	0.2972	0.0101	-0.0001	0.2745	x	x	x	x	x	x	x	x	x
Striped Maple	0.0083	0.0000	0.0922	0.5785	0.3326	0.9516	0.0049	0.0000	0.2423	x	x	x	4.6370	4.5211	4.7761
Alpha vary	0.0083	0.0000	0.0922	0.5785	0.3326	0.9516	0.0049	0.0000	0.2423	x	x	x	4.6370	4.5211	4.7761
Sugar Maple	3.1195	2.8855	3.3846	0.0199	-0.0001	0.6341	3.1802	2.6555	3.6413	8.4644	7.6603	9.1416	5.3364	4.9629	5.6566
Alpha vary	3.1195	2.8855	3.3846	0.0199	-0.0001	0.6341	3.1802	2.6555	3.6413	8.4644	7.6603	9.1416	5.3364	4.9629	5.6566
White Ash	5.1007	4.6671	5.5342	x	x	x	5.9974	5.1877	6.0273	11.0838	10.7513	11.4163	x	x	x
Alpha vary	5.1007	4.6671	5.5342	x	x	x	5.9974	5.1877	6.0273	11.0838	10.7513	11.4163	x	x	x
Yellow Birch	6.2993	6.2048	6.3938	0.0063	0.0000	0.1267	5.6552	5.0048	6.0227	8.1073	7.9046	8.3100	3.7837	3.5188	3.9729
Alpha vary	6.2993	6.2048	6.3938	0.0063	0.0000	0.1267	5.6552	5.0048	6.0227	8.1073	7.9046	8.3100	3.7837	3.5188	3.9729

b) α values with confidence limits obtained using lognormal

	All	lower	upper	Stoke	lower	upper	SutCJ01	lower	upper	SutCJ02	lower	upper	Weedon	lower	upper
Beech															
Alpha vary	3.5529	2.7357	4.2813	x	x	x	2.8820	1.1816	5.1587	4.9766	3.1850	6.0216	5.9825	5.2347	6.0124
Black Cherry															
Alpha vary	0.7193	0.0000	1.4998	x	x	x	7.4603	5.9682	8.0198	5.4267	4.5042	6.0236	x	x	x
Red Maple															
Alpha vary	0.0159	0.0000	0.2881	0.0042	0.0000	0.2582	x	x	x	x	x	x	x	x	x
Striped Maple															
Alpha vary	0.1008	0.0192	0.1850	1.3964	1.1381	1.8642	0.0508	-0.0003	0.2780	x	x	x	4.6355	4.4965	4.7746
Sugar Maple															
Alpha vary	2.9474	2.6379	3.1979	0.0213	-0.0001	0.5315	4.2596	3.9188	4.6430	7.7127	7.0185	8.0212	3.7560	3.4368	4.0565
White Ash															
Alpha vary	5.6547	5.2023	6.0506	x	x	x	8.9261	8.1227	9.0153	10.3333	9.9716	10.5916	x	x	x
Yellow Birch															
Alpha vary	1.2978	1.2004	1.3886	0.0061	0.0000	0.0888	7.7470	7.2435	8.0182	3.3982	3.1093	3.6870	3.6302	3.4305	3.8662

= not significantly different from 2.0

Appendix V:

a) STR values with confidence limits obtained using the Weibull

	Stoke	lower	upper	SutCJ01	lower	upper	SutCJ02	lower	upper	Weedon	lower	upper
Beech												
α vary	x	x	x	98.688	54.772	158.888	218.216	173.482	295.683	22.301	14.830	31.444
$\alpha=2$	x	x	x	54.854	31.267	90.784	509.940	390.104	660.372	107.685	75.380	159.913
$\alpha=2, \theta=2$	x	x	x	60.303	34.071	98.595	525.625	402.103	680.685	184.031	125.141	264.085
$\alpha=2, \theta=3$	x	x	x	75.297	41.790	120.475	744.965	569.898	964.729	259.738	174.025	367.530
Black Cherry												
α vary	x	x	x	391.693	260.476	585.580	62.082	39.732	89.087	x	x	x
$\alpha=2$	x	x	x	895.418	590.976	1329.696	178.952	116.319	262.165	x	x	x
$\alpha=2, \theta=2$	x	x	x	647.734	417.788	939.214	389.130	252.934	568.129	x	x	x
$\alpha=2, \theta=3$	x	x	x	644.739	422.304	947.766	176.255	114.566	257.333	x	x	x
Red Maple												
α vary	99556.062	84124.872	100053.842	x	x	x	x	x	x	x	x	x
$\alpha=2$	95147.853	82302.893	100380.985	x	x	x	x	x	x	x	x	x
$\alpha=2, \theta=2$	99331.329	86914.913	100324.642	x	x	x	x	x	x	x	x	x
$\alpha=2, \theta=3$	99994.398	87495.099	100494.370	x	x	x	x	x	x	x	x	x
Striped Maple												
α vary	39310.043	22996.375	58571.964	61403.406	39912.214	89648.972	x	x	x	94321.834	81116.777	100452.753
$\alpha=2$	98744.211	64087.607	100354.237	96539.372	62267.895	100400.946	x	x	x	5154.795	4407.350	5902.240
$\alpha=2, \theta=2$	98660.516	68678.144	100031.210	99533.543	68678.144	100031.210	x	x	x	8716.185	7539.500	10023.613
$\alpha=2, \theta=3$	99813.493	66375.973	100312.560	99828.110	66884.833	100327.250	x	x	x	6761.125	5848.373	7809.099
Sugar Maple												
α vary	11.490	6.262	18.154	509.168	455.705	557.539	3.296	2.077	4.450	4881.600	4320.216	5491.800
$\alpha=2$	23.833	13.346	38.371	356.994	321.295	392.693	407.732	269.103	568.785	25058.319	22176.612	28190.609
$\alpha=2, \theta=2$	22.309	12.270	35.472	512.989	461.699	561.734	305.717	204.831	432.590	12199.446	10796.510	13785.374
$\alpha=2, \theta=3$	20.506	11.688	33.732	597.398	537.659	654.151	398.567	265.047	561.980	4306.362	3811.130	4844.657
White Ash												
α vary	x	x	x	2728.063	2086.968	3451.000	582.044	477.276	721.735	x	x	x
$\alpha=2$	x	x	x	922.275	710.152	1175.900	1714.888	1371.910	2075.014	x	x	x
$\alpha=2, \theta=2$	x	x	x	987.977	755.803	1249.791	1625.998	1308.928	1975.587	x	x	x
$\alpha=2, \theta=3$	x	x	x	3763.258	2878.893	4760.522	1392.447	1120.920	1698.785	x	x	x
Yellow Birch												
α vary	1092.223	966.618	1234.212	1775.125	1491.105	2094.647	69703.625	65172.869	74582.879	54522.702	50433.500	58611.905
$\alpha=2$	34649.077	30664.433	38980.211	2419.864	2032.686	2855.439	40386.778	37963.571	43213.852	56074.645	51869.046	59999.870
$\alpha=2, \theta=2$	27225.466	24230.665	30764.777	8222.228	6906.671	9702.229	62869.294	58782.790	66955.799	44857.797	41717.752	48222.132
$\alpha=2, \theta=3$	34951.431	30757.259	39145.602	3032.354	2547.177	3578.177	34979.532	32705.863	37253.202	49519.085	46052.749	53480.612

b) STR values with confidence limits obtained using the lognormal

Beech	Stoke	lower	upper	SutCJ01	lower	upper	SutCJ02	lower	upper	Weedon	lower	upper
Alpha vary	x	x	x	2096.029	1205.217	3479.409	480.648	358.083	605.617	655.441	432.591	917.618
Alpha = 2	x	x	x	5329.916	2931.454	8474.566	388.677	295.395	499.451	1369.596	924.478	1951.675
Black Cherry												
Alpha vary	x	x	x	215.529	145.482	327.603	168.341	106.055	239.044	x	x	x
Alpha = 2	x	x	x	819.114	544.711	1228.672	997.809	643.587	1446.823	x	x	x
Red Maple												
Alpha vary	55536.195	47761.128	63311.262	x	x	x	x	x	x	x	x	x
Alpha = 2	97704.778	84514.633	100147.398	x	x	x	x	x	x	x	x	x
Striped Maple												
Alpha vary	81782.263	47433.713	100183.272	94942.685	62187.459	100164.533	x	x	x	96043.671	83557.994	100365.636
Alpha = 2	92202.518	57165.561	100039.732	99249.250	70963.214	100241.742	x	x	x	8098.166	7004.913	9353.382
Sugar Maple												
Alpha vary	17.123	10.017	29.109	266.418	243.772	297.056	8.864	6.072	12.809	553.293	486.898	619.688
Alpha = 2	164.985	93.217	269.751	367.399	332.496	404.139	520.017	358.812	759.225	2065.730	1828.171	2323.947
White Ash												
Alpha vary	x	x	x	531.765	409.459	678.000	1487.408	1182.490	1792.327	x	x	x
Alpha = 2	x	x	x	3749.911	2831.182	4706.138	1609.431	1287.545	1955.458	x	x	x
Yellow Birch												
Alpha vary	989.651	870.892	1113.357	865.113	731.020	1020.833	49520.468	48549.240	52986.900	47963.752	44846.108	51800.852
Alpha = 2	6891.627	6099.090	7753.081	2719.951	2298.359	3209.543	33467.543	31292.153	35642.933	60882.565	56316.372	65448.757

Appendix VI: Seedbed Favourabilities – values range between 0 and 1. A higher number indicates a more favourable seedbed.

Beech												
Stoke (T1,T2,T3)		Leaf Litter			Rotten Wood			Mineral			min/leaf	rotten/leaf
Function	Parameters	Conf. Limits			Conf. Limits			Conf. Limits				
Weibull	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=3$	x	x	x	x	x	x	x	x	x		
Log Normal	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
Sutton (T1,T2,T3)												
Weibull	All vary	0.19	0.08	0.35	0.55	0.00	1.00	0.28	0.00	1.00	1.48	2.89
	$\alpha=2$	0.29	0.13	0.56	0.89	0.00	1.00	0.54	0.00	1.00	1.86	3.11
	$\alpha=2;\theta=2$	0.29	0.13	0.53	0.89	0.00	1.00	0.43	0.00	1.00	1.48	3.09
	$\alpha=2;\theta=3$	0.23	0.10	0.43	0.79	0.00	1.00	0.38	0.00	1.00	1.63	3.40
Log Normal	All vary	0.48	0.23	0.88	0.56	0.00	1.00	0.75	0.00	1.00	1.56	1.17
	$\alpha=2$	0.25	0.11	0.44	0.28	0.00	1.00	0.38	0.00	1.00	1.54	1.11
Sutton (T4,T5)												
Weibull	All vary	0.36	0.23	0.46	0.35	0.00	1.00	0.71	0.52	1.00	1.99	0.96
	$\alpha=2$	0.14	0.10	0.20	0.02	0.00	0.96	0.69	0.41	1.00	4.89	0.12
	$\alpha=2;\theta=2$	0.14	0.09	0.19	0.00	0.00	0.94	0.69	0.40	1.00	5.07	0.03
	$\alpha=2;\theta=3$	0.10	0.07	0.14	0.00	0.00	0.67	0.49	0.29	0.77	5.10	0.02
Log Normal	All vary	0.15	0.10	0.20	0.01	0.00	0.75	0.63	0.34	0.96	4.27	0.04
	$\alpha=2$	0.20	0.13	0.27	0.01	0.00	1.00	0.86	0.49	1.00	4.39	0.05
Weedon (T1,T2)												
Weibull	All vary	0.59	0.37	0.84	0.04	0.00	1.00	0.79	0.00	1.00	1.35	0.06
	$\alpha=2$	0.28	0.19	0.44	0.02	0.00	1.00	0.67	0.00	1.00	2.38	0.07
	$\alpha=2;\theta=2$	0.18	0.11	0.27	0.01	0.00	1.00	0.39	0.00	1.00	2.17	0.03
	$\alpha=2;\theta=3$	0.12	0.08	0.18	0.00	0.00	0.88	0.32	0.00	0.90	2.58	0.01
Log Normal	All vary	0.22	0.14	0.31	0.02	0.00	1.00	0.30	0.00	1.00	1.38	0.09
	$\alpha=2$	0.77	0.52	1.00	0.04	0.00	1.00	0.00	0.00	1.00	0.00	0.05
Black Cherry												
Stoke (T1,T2,T3)		Leaf Litter			Rotten Wood			Mineral			min/leaf	rotten/leaf
Function	Parameters	Conf. Limits			Conf. Limits			Conf. Limits				
Weibull	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=3$	x	x	x	x	x	x	x	x	x		
Log Normal	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
Sutton (T1,T2,T3)												
Weibull	All vary	0.96	0.62	1.00	0.01	0.00	1.00	0.41	0.00	1.00	0.43	0.01
	$\alpha=2$	0.69	0.44	1.00	0.00	0.00	1.00	0.35	0.00	1.00	0.51	0.01
	$\alpha=2;\theta=2$	0.98	0.61	1.00	0.01	0.00	1.00	0.44	0.00	1.00	0.45	0.01
	$\alpha=2;\theta=3$	0.93	0.59	1.00	0.00	0.00	1.00	0.43	0.00	1.00	0.46	0.00
Log Normal	All vary	0.85	0.55	1.00	0.11	0.00	1.00	0.40	0.00	1.00	0.47	0.12
	$\alpha=2$	0.63	0.40	0.98	0.01	0.00	1.00	0.43	0.00	1.00	0.68	0.02
Sutton (T4,T5)												
Weibull	All vary	0.31	0.18	0.47	0.07	0.00	1.00	0.41	0.00	1.00	1.32	0.21
	$\alpha=2$	0.35	0.20	0.55	0.07	0.00	1.00	0.75	0.06	1.00	2.17	0.20
	$\alpha=2;\theta=2$	0.17	0.10	0.27	0.12	0.00	1.00	0.30	0.01	0.80	1.75	0.72
	$\alpha=2;\theta=3$	0.45	0.27	0.70	0.01	0.00	1.00	0.55	0.00	1.00	1.21	0.03
Log Normal	All vary	0.10	0.05	0.17	0.31	0.00	1.00	0.65	0.20	1.00	6.41	3.04
	$\alpha=2$	0.08	0.04	0.14	0.20	0.00	1.00	0.63	0.23	1.00	7.83	2.54
Weedon (T1,T2)												
Weibull	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=3$	x	x	x	x	x	x	x	x	x		
Log Normal	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		

Red Maple												
Stoke (T1,T2,T3)		Leaf Litter			Rotten Wood			Mineral			min/leaf	rotten/leaf
Function	Parameters	Conf. Limits			Conf. Limits			Conf. Limits				
Weibull	All vary	0.01	0.01	0.02	0.00	0.00	0.02	0.00	0.00	0.01	0.29	0.07
	$\alpha=2$	0.03	0.02	0.03	0.00	0.00	0.05	0.01	0.00	0.03	0.38	0.10
	$\alpha=2;\theta=2$	0.02	0.02	0.02	0.00	0.00	0.03	0.01	0.00	0.02	0.37	0.02
	$\alpha=2;\theta=3$	0.02	0.01	0.02	0.00	0.00	0.03	0.00	0.00	0.02	0.29	0.02
Log Normal	All vary	0.01	0.01	0.01	0.00	0.00	0.02	0.00	0.00	0.01	0.21	0.04
	$\alpha=2$	0.01	0.01	0.01	0.00	0.00	0.02	0.00	0.00	0.01	0.10	0.03
Sutton (T1,T2,T3)												
Weibull	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=3$	x	x	x	x	x	x	x	x	x		
Log Normal	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
Sutton (T4,T5)												
Weibull	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=3$	x	x	x	x	x	x	x	x	x		
Log Normal	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
Weedon (T1,T2)												
Weibull	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=3$	x	x	x	x	x	x	x	x	x		
Log Normal	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
Striped Maple												
Stoke (T1,T2,T3)		Leaf Litter			Rotten Wood			Mineral			min/leaf	rotten/leaf
Function	Parameters	Conf. Limits			Conf. Limits			Conf. Limits				
Weibull	All vary	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.01	0.11	0.64
	$\alpha=2$	0.02	0.01	0.03	0.01	0.00	0.44	0.00	0.00	0.05	0.21	0.38
	$\alpha=2;\theta=2$	0.65	0.34	1.00	0.98	0.07	1.00	0.90	0.27	1.00	1.39	1.52
	$\alpha=2;\theta=3$	0.01	0.00	0.01	0.00	0.00	0.05	0.00	0.00	0.02	0.16	0.02
Log Normal	All vary	0.01	0.00	0.01	0.01	0.00	0.06	0.00	0.00	0.01	0.03	1.56
	$\alpha=2$	0.01	0.00	0.01	0.00	0.00	0.06	0.00	0.00	0.02	0.11	0.24
Sutton (T1,T2,T3)												
Weibull	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=3$	x	x	x	x	x	x	x	x	x		
Log Normal	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
Sutton (T4,T5)												
Weibull	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=3$	x	x	x	x	x	x	x	x	x		
Log Normal	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
Weedon (T1,T2)												
Weibull	All vary	0.94	0.78	1.00	0.91	0.00	1.00	0.96	0.50	1.00	1.03	0.98
	$\alpha=2$	0.58	0.49	0.67	0.16	0.00	1.00	0.86	0.38	1.00	1.50	0.28
	$\alpha=2;\theta=2$	0.36	0.30	0.42	0.04	0.00	1.00	0.57	0.27	0.95	1.59	0.12
	$\alpha=2;\theta=3$	0.45	0.38	0.53	0.06	0.00	1.00	0.69	0.32	1.00	1.53	0.13
Log Normal	All vary	0.72	0.61	0.85	0.99	0.00	1.00	0.69	0.27	1.00	0.96	1.37
	$\alpha=2$	0.36	0.30	0.42	0.76	0.00	1.00	0.52	0.23	0.89	1.46	2.12

Sugar Maple												
Stoke (T1,T2,T3)		Leaf Litter			Rotten Wood			Mineral			min/leaf	rotten/leaf
Function	Parameters	Conf. Limits			Conf. Limits			Conf. Limits				
Weibull	All vary	0.74	0.40	1.00	0.48	0.00	1.00	0.01	0.00	1.00	0.02	0.66
	$\alpha=2$	0.90	0.50	1.00	0.03	0.00	1.00	0.03	0.00	1.00	0.03	0.04
	$\alpha=2;\theta=2$	0.96	0.53	1.00	0.00	0.00	1.00	0.00	0.00	1.00	0.00	0.01
	$\alpha=2;\theta=3$	0.99	0.56	1.00	0.04	0.00	1.00	0.00	0.00	1.00	0.00	0.04
Log Normal	All vary	0.47	0.28	0.81	0.07	0.00	1.00	0.01	0.00	0.92	0.03	0.14
	$\alpha=2$	0.58	0.33	0.96	0.06	0.00	1.00	0.00	0.00	0.65	0.01	0.09
Sutton (T1,T2,T3)												
Weibull	All vary	0.32	0.29	0.35	0.57	0.32	0.81	0.00	0.00	0.03	0.00	1.77
	$\alpha=2$	0.51	0.46	0.57	0.83	0.50	1.00	0.00	0.00	0.05	0.00	1.61
	$\alpha=2;\theta=2$	0.36	0.32	0.40	0.60	0.34	0.87	0.00	0.00	0.03	0.00	1.65
	$\alpha=2;\theta=3$	0.31	0.28	0.34	0.50	0.30	0.75	0.00	0.00	0.03	0.00	1.62
Log Normal	All vary	0.50	0.45	0.56	0.73	0.44	1.00	0.00	0.00	0.03	0.00	1.46
	$\alpha=2$											
Sutton (T4,T5)												
Weibull	All vary	0.49	0.25	0.68	0.55	0.00	1.00	0.93	0.25	1.00	1.89	1.13
	$\alpha=2$	0.03	0.02	0.05	0.74	0.14	1.00	0.14	0.05	0.29	4.58	23.63
	$\alpha=2;\theta=2$	0.04	0.02	0.07	0.96	0.21	1.00	0.21	0.08	0.42	5.46	24.84
	$\alpha=2;\theta=3$	0.03	0.02	0.05	0.72	0.15	1.00	0.15	0.06	0.31	4.91	22.82
Log Normal	All vary	0.21	0.12	0.32	0.97	0.00	1.00	0.24	0.04	0.62	1.15	4.72
	$\alpha=2$	0.03	0.01	0.05	0.71	0.20	1.00	0.17	0.06	0.33	6.17	26.11
Weedon (T1,T2)												
Weibull	All vary	0.24	0.20	0.27	0.00	0.00	0.18	0.98	0.72	1.00	4.15	0.01
	$\alpha=2$	0.09	0.07	0.10	0.00	0.00	0.07	0.36	0.26	0.47	4.14	0.00
	$\alpha=2;\theta=2$	0.18	0.15	0.21	0.00	0.00	0.15	0.73	0.53	0.96	4.07	0.00
	$\alpha=2;\theta=3$	0.04	0.03	0.05	0.00	0.00	0.03	0.15	0.11	0.20	3.73	0.00
Log Normal	All vary	0.23	0.19	0.27	0.00	0.00	0.23	0.94	0.68	1.00	4.13	0.01
	$\alpha=2$	0.09	0.07	0.10	0.00	0.00	0.07	0.37	0.27	0.48	4.39	0.01
White Ash												
Stoke (T1,T2,T3)		Leaf Litter			Rotten Wood			Mineral			min/leaf	rotten/leaf
Function	Parameters	Conf. Limits			Conf. Limits			Conf. Limits				
Weibull	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=3$	x	x	x	x	x	x	x	x	x		
Log Normal	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
Sutton (T1,T2,T3)												
Weibull	All vary	0.35	0.24	0.48	0.54	0.00	1.00	0.68	0.30	1.00	1.94	1.55
	$\alpha=2$	0.43	0.31	0.59	0.16	0.00	1.00	0.75	0.34	1.00	1.72	0.37
	$\alpha=2;\theta=2$	0.46	0.33	0.63	0.32	0.00	1.00	0.78	0.36	1.00	1.69	0.68
	$\alpha=2;\theta=3$	0.11	0.08	0.15	0.09	0.00	0.44	0.19	0.09	0.32	1.70	0.80
Log Normal	All vary	0.31	0.22	0.42	0.23	0.00	1.00	0.61	0.30	1.00	1.95	0.73
	$\alpha=2$	0.11	0.07	0.14	0.03	0.00	0.32	0.14	0.06	0.25	1.34	0.29
Sutton (T4,T5)												
Weibull	All vary	0.03	0.02	0.04	0.27	0.05	0.65	0.32	0.23	0.44	11.18	9.49
	$\alpha=2$	0.08	0.05	0.10	0.72	0.12	1.00	0.78	0.56	1.00	10.16	9.48
	$\alpha=2;\theta=2$	0.07	0.05	0.10	0.79	0.14	1.00	0.79	0.55	1.00	10.69	10.66
	$\alpha=2;\theta=3$	0.09	0.06	0.12	0.94	0.16	1.00	0.90	0.64	1.00	10.40	10.82
Log Normal	All vary	0.10	0.07	0.14	0.74	0.01	1.00	0.92	0.63	1.00	9.16	7.37
	$\alpha=2$	0.14	0.10	0.20	0.89	0.00	1.00	0.95	0.65	1.00	6.58	6.15
Weedon (T1,T2)												
Weibull	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=2$	x	x	x	x	x	x	x	x	x		
	$\alpha=2;\theta=3$	x	x	x	x	x	x	x	x	x		
Log Normal	All vary	x	x	x	x	x	x	x	x	x		
	$\alpha=2$	x	x	x	x	x	x	x	x	x		

Yellow Birch												
Stoke (T1,T2,T3)		Leaf Litter			Rotten Wood			Mineral			min/leaf	rotten/leaf
Function	Parameters	Conf. Limits			Conf. Limits			Conf. Limits				
Weibull	All vary	0.10	0.08	0.12	0.01	0.00	0.27	0.86	0.71	1.00	8.50	0.07
	$\alpha=2$	0.10	0.08	0.13	0.00	0.00	0.23	0.98	0.81	1.00	9.59	0.03
	$\alpha=2;\theta=2$	0.10	0.08	0.13	0.00	0.00	0.22	1.00	0.82	1.00	9.86	0.00
	$\alpha=2;\theta=3$	0.10	0.08	0.12	0.00	0.00	0.22	0.95	0.77	1.00	9.85	0.00
Log Normal	All vary	0.15	0.12	0.17	0.00	0.00	0.35	0.71	0.56	0.87	4.84	0.02
	$\alpha=2$	0.10	0.08	0.12	0.00	0.00	0.23	0.96	0.79	1.00	9.36	0.02
Sutton (T1,T2,T3)												
Weibull	All vary	0.07	0.04	0.10	0.00	0.00	0.09	0.82	0.66	1.00	11.47	0.02
	$\alpha=2$	0.09	0.06	0.12	0.00	0.00	0.09	0.95	0.75	1.00	10.86	0.01
	$\alpha=2;\theta=2$	0.04	0.03	0.06	0.00	0.00	0.05	0.51	0.41	0.64	11.79	0.01
	$\alpha=2;\theta=3$	0.08	0.05	0.11	0.00	0.00	0.08	0.91	0.72	1.00	11.42	0.00
Log Normal	All vary	0.06	0.04	0.09	0.00	0.00	0.08	0.60	0.47	0.75	9.38	0.00
	$\alpha=2$	0.06	0.04	0.09	0.00	0.00	0.09	0.94	0.76	1.00	15.85	0.02
Sutton (T4,T5)												
Weibull	All vary	0.00	0.00	0.00	0.07	0.02	0.13	0.91	0.85	0.97	690.96	49.71
	$\alpha=2$	0.00	0.00	0.00	0.06	0.02	0.12	0.82	0.77	0.88	792.86	59.69
	$\alpha=2;\theta=2$	0.00	0.00	0.00	0.04	0.02	0.08	0.55	0.52	0.59	694.26	50.07
	$\alpha=2;\theta=3$	0.00	0.00	0.00	0.07	0.03	0.14	0.96	0.89	1.00	698.73	51.18
Log Normal	All vary	0.00	0.00	0.00	0.04	0.02	0.08	0.48	0.45	0.51	486.34	43.30
	$\alpha=2$	0.00	0.00	0.00	0.08	0.03	0.14	0.88	0.82	0.94	591.08	51.85
Weedon (T1,T2)												
Weibull	All vary	0.00	0.00	0.01	0.58	0.40	0.81	0.93	0.85	1.00	189.11	118.26
	$\alpha=2$	0.00	0.00	0.01	0.25	0.15	0.37	0.70	0.64	0.75	199.89	72.50
	$\alpha=2;\theta=2$	0.00	0.00	0.01	0.32	0.20	0.47	0.84	0.78	0.92	201.26	77.29
	$\alpha=2;\theta=3$	0.00	0.00	0.01	0.29	0.18	0.43	0.77	0.72	0.84	206.78	78.06
Log Normal	All vary	0.01	0.00	0.01	0.61	0.41	0.84	0.97	0.90	1.00	150.79	94.42
	$\alpha=2$	0.00	0.00	0.00	0.32	0.20	0.45	0.91	0.84	0.98	472.02	165.28