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Individual-Based Models and Scaling Methods for Ecological Forestry: Implications of Tree Phenotypic Plasticity

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1. Introduction

The concept of sustainable forest management (SFM) has been developed across traditional disciplinary boundaries, including natural resource management, environmental, social, political, economical, climatic sciences and ecology. The Montreal process (www.mpci.org) has established multidisciplinary criteria for the SFM of temperate and boreal forests. In parallel with the Montreal process, the pan-European forest policy process (www.foresteurope.org, Forest Europe, The Ministerial Conference on the Protection of Forests in Europe, MCPFE) has developed criteria for SFM in Europe. Practical implementation of SFM criteria requires the development of scaling methods to link individual-level processes, pollution effects, climatic changes and silvicultural operations to large-scale ecosystem patterns and processes. A general problem is that data obtained in numerous experimental studies that address effects at the individual level cannot be translated to the ecosystem level without a large amount of uncertainty. Forested ecosystems have a complicated spatially heterogeneous hierarchical structure emerging from numerous interdependent individual processes. The fundamental ecological questions are how macroscopic patterns emerge as a result of self-organization of individuals and how ecosystems respond to different types of environmental disturbances occurring at different scales (Levin, 1999).

The SFM employs the ecological forestry (EF) silvicultural approach, which is significantly distinct from the intensive (traditional) forestry and, therefore, requires different modeling tools than traditional forestry models. Traditional or intensive forestry is focused on wood production to maximize productivity of land use and usually involves tree plantations of commercially important trees (Nyland, 1996; Perry, 1998). Different silvicultural tools help increase wood fiber production. In particular, use is made of fast growing and disease resistant cultivars, vegetation control via thinning and regeneration harvesting techniques, soil management, and forest pests and noncrop vegetation control. Intermediate cutting operations include low, crown and mechanical thinning target future stand growth on higher valued trees to improve the stand yield at final harvest while providing some financial return on the shorter time scales. Traditional forestry also employs prescribed fire, cutting and application of herbicides for regulation of species composition and promoting growth of economically important tree species in the mixed stands.

This chapter is focused on modeling tools for the SFM and EF. The objective of this approach is the optimization of land use (such as wood production and carbon storage) while maintaining biocomplexity of forested ecosystems. The models discussed in this chapter are to be implemented within the SFM framework to optimize land use (such as wood production and carbon storage with the criteria 2 and 5 of Montreal process "Maintenance of productive capacity of forest ecosystems" and "Maintenance of forest contribution to global carbon cycles", respectively; and criteria 1 and 3 of the MCPFE process (Ministerial Conference on the Protection of Forests in Europe) "Maintenance and appropriate enhancement of forest resources and their contribution to global carbon cycles" and "Maintenance and encouragement of productive functions of forests", respectively. The fundamental challenge for ecological forestry is to effectively manage a forest - complex ecological system, rather than a plantation of trees as in the traditional forestry approach. The biocomplexity challenges for ecological forestry are the understanding of why different plant species coexist, and which forces drive forest community structure and dynamics. One of the keystones of ecological forestry is the development of forest management systems in concert with natural processes in forested ecosystems, such as natural disturbances, forest dynamics and succession (Franklin et al., 2007). In particular, development of regeneration harvest approaches that have ecological effects similar to natural disturbances has been considered crucial for ecological forestry. Natural disturbances may occur at different spatial scales resulting in heterogeneity of forested ecosystems. The most common natural disturbances include wind-related disturbances on the individual (forest gaps) and large-scale (for example created by hurricanes and tornadoes), fire-related disturbances, and pest or disease related disturbances. These disturbances may significantly alter ecosystem structure and dynamics; however even the most dramatic events do not completely destroy ecosystems. Certain biological patterns or biological legacies, specific for each type of disturbance, remain unchanged and facilitate forest post-disturbance recovery.

Forest heterogeneity, which emerges as the result of various disturbances, is an essential element of ecological forestry, in contrast to the traditional approach, where stands are spatially homogeneous to reduce tree competition and improve timber quality (Oliver & Larson, 1996). Morphological plasticity allows trees to compete with neighbors and survive in a heterogeneous environment. In particular, open-growing trees, as well as trees growing in plantations without intense crown competition, tend to have symmetrical crowns, straight trunks, and, as a result, high quality timber. Trees growing in mixed spatially heterogeneous stand tend to exhibit plasticity patterns as every individual tree needs to adjust to its local unique neighborhood. These trees have much less value in term of timber than plantation trees. Such trees often have non-symmetrical crowns and curved trunks as they lean towards sunlight due to intense individual tree competition.

Forested ecosystems demonstrate multiple-scale self-organization patterns in response to disturbances. At present, we lack the predictive modeling tools that can combine the effects of forest disturbances occurring at different scales. An ideal model would present an analytically tractable model predicting landscape-level vegetation dynamics using individual ecophysiological traits as variables and available forest survey data as initial conditions. How can we develop such models?

Simon Levin, in a seminal paper (Levin, 2003), considered a modern theoretical approach to multiscale ecological modeling. In particular, he introduced ecological systems as complex adaptive systems which result from self-organization on multiple levels, where individual organisms are linked through interactions between each other and the abiotic environment. In this chapter the framework of complex adaptive systems is applied to forest ecology

and management. The forest is considered as a complex adaptive system (as a mosaic of individual plants, each of which grows adaptively in its biotic and abiotic environment in dynamic interaction with its neighbors). These interactions occur simultaneously at different temporal and spatial scales, both above and below ground, and lead to the development of self-organized patterns and structural complexity. The central question of this chapter is how forest patterns emerge as a result of the self-organization of individual trees. Individual tree plasticity is a critical process for forest modeling, though it has previously not been taken into account. The plasticity patterns of tree crowns in response to light competition enable directional growth toward available light, and lead to tree asymmetries caused by stem inclinations and inhomogeneous branch growth. Recently developed individual-based forest simulators, Crown Plastic SORTIE (Strigul et al., 2008) and LES, focus on forest self-organization at the stand level. These models, by incorporating individual crown plasticity, predict substantially different macroscopic patterns than do previous models (regularity in canopy spatial structure, for instance, which has only recently been noticed in field studies). Most importantly, the simulator's structure allows to derive an accurate approximation of the individual-based model, the Perfect Plasticity Approximation (PPA). This macroscopic system of equations predicts the large-scale behavior of the individual-based forest simulator, using the same parameter values and functional forms (Strigul et al., 2008). In particular, the PPA offers good predictions for 1) stand-level attributes, such as basal area, tree density, and size distributions; 2) biomass dynamics and self-thinning; and 3) ecological patterns, such as succession, invasion, and coexistence.

This chapter also introduces a theoretical framework for the scaling of forest spatial dynamics from individual to the landscape level based on the PPA model. The major objective of this approach is to scale up forest heterogeneity patterns across the forest hierarchy. The major idea is that the forest dynamics at the landscape level can be modeled by separating dynamics within forest stands caused by individual-level disturbances from the dynamics of the stand dynamics caused by large disturbances. The model, called Matreshka (after the Russian nesting doll) employs the PPA model as an intermediate step of scaling from the individual level to the forest stand level (or patch level). To describe the patch dynamics at the next hierarchal level, i.e., the forest stand mosaic, we employ the patch-mosaic modeling framework (Strigul et al., 2012). The Markov chain model for the mosaic of forest stands in the Lake states (MI, Wi, and MN) has been recently parameterized using the FIA data (Strigul et al., 2012). The Matreshka model unites already known models and uses the notion of ecological hierarchy that has been widely employed in landscape ecology (Bragg et al., 2004; Clark, 1991; Wu & Loucks, 1996).

The chapter consists of three sections: Section 2 introduces tree morphological plasticity as a fundamental pattern for the canopy self-organization. In section 3 the individual-based modeling approach is considered with a special focus on the development of the Crown Plastic SORTIE model, LES, and PPA models. Section 4 introduces a theoretical framework for the scaling of forest dynamics from individual to the landscape level based on the PPA model.

2. Individual tree plasticity and canopy self-organization

2.1 Crown plasticity and leaning of individual trees

In competing for light, trees invest carbon and other resources to achieve such above-ground form as will provide them with enough light for photosynthesis. To achieve this goal, individual trees demonstrate amazing phenotypic plasticity, using advantages of modular organization (Ford, 1992). Numerous factors constrain tree development, for instance, gravity
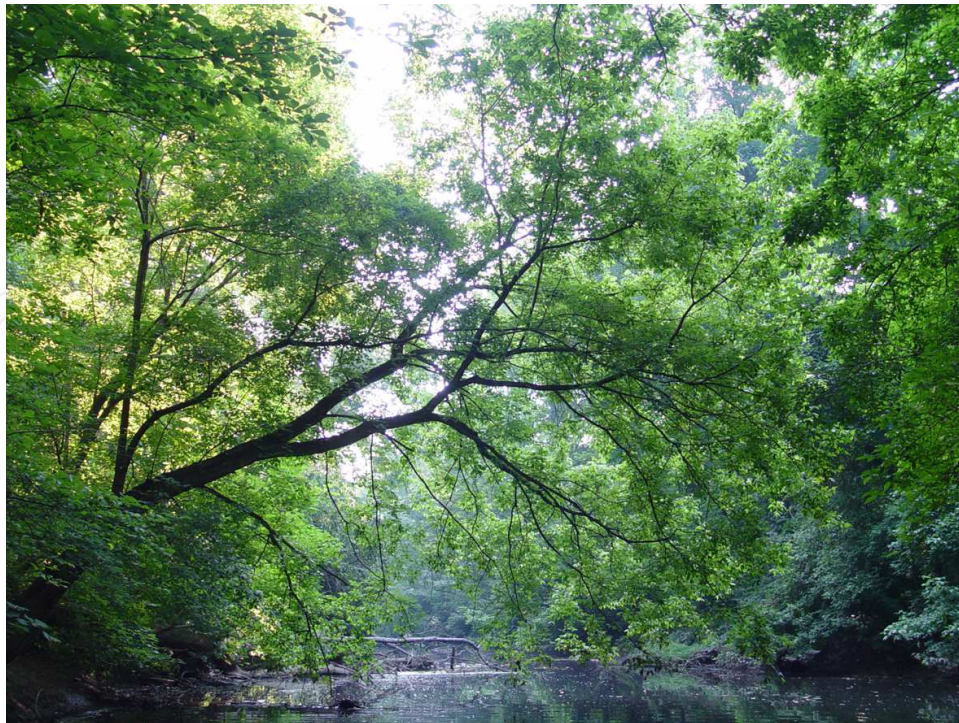
Fig. 1. Tree growing across a small forest river. A typical example of tree plasticity and "riverside behavior". The Institute for Advanced Study Woods (Princeton, NJ).

(McMahon & Kronauer, 1976) and other abiotic factors such as wind (Grace, 1977) and snow (King & Loucks, 1978), neighborhood effects (Ford, 1992), and, also genetic and physiological constraints such as the need to provide an efficient connection between their own above- and below-ground parts (Kleunen & Fischer, 2005). One permanent goal of a given individual tree is to develop an optimal crown under the current limitations in the dynamic environment. This includes different wood-allocation strategies in open-growing trees and trees in dense stands (Holbrook & Putz, 1989), as well as the development of sun branches and the degradation or physiological modification of shaded branches (Stoll & Schmid, 1998).

The physiological mechanisms underlying plant-phenotypic plasticity and phototropism have received significant attention in recent decades, yet many phenomena remain unclear (Firn, 1988; Kleunen & Fischer, 2005). Apical control can partially explain interspecific differences in tree leaning, crown shapes, and also differences in growth patterns between understory and overstory trees (Loehle, 1986; Oliver & Larson, 1996). Plants have also a variety of photosensory systems to detect their neighbors and select an optimal growing strategy. A better-investigated, phytochrome-signaling mechanism triggers some adaptive morphological changes such as adaptive branching (Stoll & Schmid, 1998) and stem elongation (Ballaré, 1999) in response to the alterations in far-red radiation caused by the reflection of sunlight by neighbor plants.

Tree-plasticity patterns relating to the competition for light and phototropism include the development of an asymmetrical crown, as a result of both the growth of individual branches and the phototropism of the whole tree (resulting in trunk elongation and inclinations). Tree-plasticity patterns caused by competition for light are more pronounced near forest margins, such as road cuts or riverbanks (Fig. 1). At these places trees develop asymmetric crowns and lean toward the gap, this pattern was called "riverside behavior" (Loehle, 1986).

Crown asymmetries and tree leaning can be also caused by factors not related to light competition, for example, soil creep (Harker, 1996), wind (Lawrence, 1939), and destruction of the apical meristem by insects. Trees growing on hillsides often have special trunk inclinations induced by soil creep, which geologists call a "d" curve (Harker, 1996). In this case, the base of the tree trunk starts at an angle to the vertical, with this angle continuously decreasing toward the top of the tree. However, such trees can have symmetrical crowns. This type of curved trunk is used as an indicator of soil creep. It was suggested that downward trunk inclinations of understory trees growing on the slope may have adaptive significance for light competition (Ishii & Higashi, 1997), however other authors disagree with this hypothesis (Loehle, 1997).

While crown asymmetry and trunk inclination represent two closely related patterns providing for tree morphological plasticity in light competition, the development of asymmetrical crown has received more attention than the tree leaning process. It was recognized since the earliest stages of the forest science development that an understanding of how tree crown is changed in competition for light is critical for forest growth predictions (Busgen & Munch, 1929; Reventlow, 1960). Tree crown area is naturally connected with total leaf surface, photosynthetic activity, carbon gain, and tree growth (Assmann, 1970; Smith et al., 1997). Crown competition is analyzed using crown class classification, individual tree zone of influence and by computing different competition indices. In forestry practice these methods are applied under the implicit assumption that trees grow vertically and the center of the zone of influence is also the center of tree growth. This is an important assumption in silviculture, since traditional foresters typically considered curved-trunk trees to be abnormal and unconditioned, and ignored them (Macdonald & Hubert, 2002; Westing & Schulz, 1965). Methods to measure such trees were also not developed (Grosenbaugh, 1981). The main objective of traditional silviculture to produce qualitative wood from well-formed trees (i.e., trees with symmetrical crowns and straight stems). Therefore for foresters tree leaning is in fact a problem which causes the development of bad-formed trees, rather than an important ecological property (Macdonald & Hubert, 2002). Typical planting and thinning regimes in silviculture significantly reduce the frequency of trunk inclinations (Assmann, 1970; Oliver & Larson, 1996; Smith et al., 1997). Only a few studies are concerned with adaptive trunk inclinations associated with the phototropism of the whole tree. In the beginning of the last century these patterns were described by German forester Arnold Engler (Engler, 1924). More recently, Loehle (Loehle, 1986) reported connections between trunk inclinations and the phototropism of the whole tree, based on data collected in Georgia and Washington State.

2.2 Gap dynamics and community-level patterns

Forest gaps are defined as small, localized disturbances, such as treefalls, which cause asynchronous local-forest regeneration processes (Oliver & Larson, 1996). In contrast, large-scale catastrophic disturbances, such as hurricanes or clearcutting, cause synchronized forest regenerations on the stand level. Gap dynamics is an important ecological process in which tree-plasticity patterns are exhibited (Fig. 2). Since forest gap dynamics constitutes a major process of regeneration, succession, and species coexistence (McCarthy, 2001; Ryel & Beyschlag, 2000), tree plasticity patterns can be associated with major trade-offs determining the strategies of trees.

Typically, large trees located at the gap border extend their crowns toward the gap (Hibbs, 1982) significantly reducing gap size and affecting canopy recruitment (Frelich & Martin, 1988). Gap closure, in turn, involves an interplay between two processes. The first process consists of lateral gap closure, brought about by crown encroachments of large trees at the
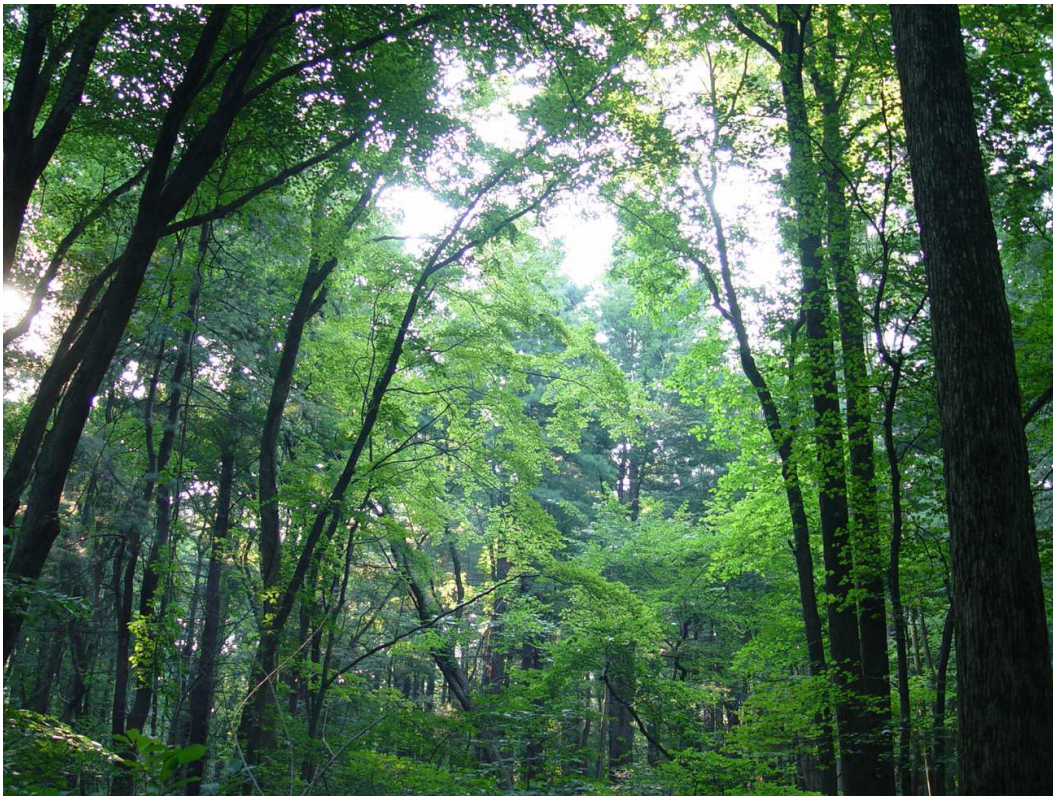
Fig. 2. A typical forest gap in the Institute for Advanced Study Woods (Princeton, NJ). Trees growing on the gap boundaries demonstrate plasticity patterns and phototropism, they modify their crowns and lean toward the gap.

gap borders and growth; the second process involves the crown development of small trees in the gap. The relative contributions of these two processes can be regulated by the gap size and species composition of both saplings and neighbor trees. To capture a small gap, saplings must be able to grow fast enough to compete with expanding crowns of dominant and co-dominant trees at the gap borders; in large gaps, by contrast, saplings have more opportunities to establish a canopy (Cole & Lorimer, 2005; Gysel, 1951; Webster & Lorimer, 2005; Woods & Shanks, 1959).

Individual tree plasticity leads to the development of a regular spatial canopy structure; in particular, crown centers are spaced more evenly than are the bases of plants. This pattern was reported for natural forest stands on Hokkaido (Ishizuka, 1984), and in the pure stand of *Atherosperma moschatum Labillardiere* (Monimiaceae) in Tasmania (Olesen, 2001), where crown-center distributions of all canopy were close to the uniform. Similar patterns were also discovered in the natural mature *Pinus sylvestris L.* forest in Eastern Finland (Rouvinen & Kuuluvainen, 1997); however, in that case the direction of crown asymmetry was strongly weighted in a southern and southwestern direction, which is the direction of most abundant solar radiation. It was suggested that in this forest, both factors, i.e., light competition with neighbors and phototropism toward the south, led to crown asymmetry and regular crown spacing patterns (Rouvinen & Kuuluvainen, 1997). Regular spacing of crowns in the canopy has been also established in computer simulations, where individual plants are able to exhibit adaptive crown plasticity (Strigul et al., 2008; Umeki, 1995a). However, forest simulators that does not include tree plasticity do not predict canopy regularity (Strigul et al., 2008).

2.3 Interspecific differences and cost of tree plasticity

Most tree species of different systematic and ecological groups demonstrate some tree plasticity patterns. It has been reported, for instance, for conifers (Loehle, 1986; Stoll & Schmid, 1998; Umeki, 1995b) and broad-leaf trees (Brisson, 2001; Woods & Shanks, 1959), in tropical (Young & Hubbell, 1991) and temperate forested ecosystems (Frelich & Martin, 1988; Gysel, 1951; Stoll & Schmid, 1998; Webster & Lorimer, 2005). At the same time, different tree species vary significantly in their ability to execute plasticity patterns; this raises questions concerning the different life histories and ecological strategies associated with tree plasticity and light competition. In particular, gap closure by crown encroachment of adjacent dominant and co-dominant trees was reported to be a typical process in the replacement of chestnut (*Castanea dentate* (Marsh.) Borkh.) by *Quercus prinus* L. and *Q. rubra* L. in the Great Smoky Mountains (Woods & Shanks, 1959). Northern red oak *Q. rubra* L. significantly surpassed yellow poplar (*Liriodendron tulipifera* L.) in its capacity for crown encroachment (lateral extension rates are 16.5 cm/year and 9.2 cm/year respectively) in Appalachian hardwood stands (Trimble & Tryon, 1966). The average lateral crown growth toward the small tree gaps of seven tree species in hemlock-hardwood forests in Massachusetts varied from 6 to 14 cm/year (Hibbs, 1982). *Quercus rubra* L. demonstrated the fastest lateral crown growth, with an average 14.03 ± 1.65 cm/year and a maximum 26.4 cm/year. The other six species were ranked according to their average lateral crown growth (in cm/year) toward the gap, as follows: *Betula papyrifera* Marsh. $10.87 \pm 1.39 > B. lenta$ L. and *B. alleghaniensis* Britt. $10.68 \pm 1.58 > Tsuga\ Canadensis$ (L.) Carr. $10.68 \pm 1.58 > Acer\ rubrum$ L. $8 \pm 0.72 > Pinus\ strobus$ L. 6.10 ± 0.94. Average annual crown lateral extensions toward the gaps of 13 tree species in the Southern Appalachians (Runkle & Yetter, 1987), varied from 8.6 cm/year (*Fraxinus americana* L.) and 13.1 cm/year (*Tsuga Canadensis* (L.) Carr.) to 31.4 cm/year (*Magnolia fraseri* Walt.) and 28.7 cm/year (*Acer rubrum* L.). Three species had shown a lateral extension rate of more than 20 cm/year (*B. alleghaniensis* Britt. 22.3 cm/year, *Liriodendron tulipifera* L. 21.8 cm/year, and *Acer saccharum* 20.8 cm/year Marsh.), and the other six broad-leaved tree species showed very similar rates of $17.1 - 18.8$ cm/year (Runkle & Yetter, 1987). This brief review demonstrates that lateral crown growth rate toward the gap can vary between the stand and tree species. While some species (for example, *Q. rubra* L.) typically demonstrate more plasticity than others, many species exhibit similar patterns, and some (for example, *T. Canadensis* (L.) Carr.) apparently have much less ability to extend their crowns toward the gap. These estimates are employed in the LES model (section 3.2)

German foresters' studies of the first half of the 20th century (see Engler (1924), Busgen & Munch (1929) p. 41, Assmann (1970) pp. 244, 284, 348 and subsequent references) found that conifer trees are less plastic than broad-leaved trees, which are capable of filling highly variable types of growing space. To account for these differences, it was suggested that broad-leaved trees, such as oaks and beeches, exhibit more phototropism than conifers, such as spruces and silver firs, which have "extremely energetic geotropism" (Assmann, 1970; Busgen & Munch, 1929). This conclusion is supported by the later studies (Loehle, 1986; Umeki, 1995b). It was suggested that the contrast plasticity patterns of conifers and broad-leave trees can be explained by the apical control differences (Loehle, 1986; Waller, 1986).

One important open problem is the lack of quantitative estimates of physiological traits associated with tree plasticity. Gravity is the universal force affecting tree form and growth. This force favors a vertical trunk and a symmetrical crown, which compose the typical

form for an open growing tree. In this case the crown center of mass and the tree base are located on the same vertical line, which is the axis of tree symmetry. The execution of tree plasticity patterns, such as adaptive growth of branches and tree leaning, results in tree asymmetries and changes of the crown mass center that can make the tree less stable. Then, crown asymmetries and tree leaning should have some additional cost per tree compared to a symmetrical crown expansion (Busgen & Munch, 1929; Olesen, 2001). In a wet lowland tropical forest, tree asymmetry can increase the likelihood of the tree fall (Young & Hubbell, 1991). Tree anatomy studies and mechanical considerations show that the development of tree asymmetry causes stem tensions which should correlate with the development of additional structural tissues (Ford, 1992; McMahon & Kronauer, 1976). Umeki (Umeki, 1995a) assumed that the cost of tree asymmetry can be expressed by a reduction of tree height proportionally to the distance of the crown center movement. This assumption is also made in the Crown Plastic SORTIE and LES models (section 3.2). Loehle (Loehle, 1997) assumed that small trees with an elastic trunk can grow at an angle at practically no cost, and suggested that cost estimations are important only for large trees.

3. Scaling of vegetation dynamics: from individual trees to forest stands

The mainstream research approach in modern forestry is to use mathematical modeling in concert with experimental approaches. Certain limitations of experimental approaches make mathematical modeling especially useful. In particular, in experimental studies it is often necessary to concentrate on one focal level of organization while ignoring processes at other scales. Conclusive experimental results to support land-management decisions on different silvicultural techniques may not be obtained on a reasonable time scale and can be too expensive. Despite the availability of different forest models for use in either traditional forestry or in ecological studies, these models are often not suitable for ecological forestry. Forest yield tables is one of the oldest biological models with more than a 200-year history of development and practical applications to plantations with reduced tree competition (Mitchell, 1975; Shugart, 1984). However, forest yield tables is of an empirical nature and limited applications to more spatially heterogeneous silvicultural systems with intensive crown competition. Individual-based models (IBMs) simulating stand development emerged in the 1960s, when computer technology allowed for doing spatially-explicit simulations. Spatially explicit models can incorporate processes that occur at different scales and predict the dynamics of a forest by predicting each individual's birth, dispersal, reproduction and death and how these events are affected by spatial competition for resources with neighbors. Forest growth IBMs were developed in different directions. Foresters have developed stand simulators in order to estimate and optimize stand production; meanwhile, ecologists needed tools to study succession, species coexistence, and dynamics of indigenous forests. This difference in initial goals is reflected in the model structures, as forester and ecological models each concentrate on different aspects of forest development. Ecological models, such as the family of gap models originated from JABOVA include detailed descriptions of ecological processes which are considered to be most important, such as succession and gap dynamics (Botkin, 1993; Shugart, 1984). Forester IBMs, such as TASS (Mitchell, 1975), focus on overstory dynamics and on detailed descriptions of individual tree growth in the given neighborhood, which is important for plantations, ignoring seed production, gap and understory dynamics.

3.1 Individual-based forest simulators and tree plasticity

With respect to crown competition, individual-based forest simulators embody a wide range of assumptions. JABOVA-FORET models and many of their descendants, such as gap models, are based on the premise that a forest can be represented as a mosaic of homogeneous patches, i.e., gaps, each of which can be modeled independently. The size of every gap is usually assumed to be equal to the size of one large overstory tree. These patches have a horizontally homogeneous structure-i.e., the crowns of all trees in a gap extend horizontally over each patch (Botkin, 1993; Bugmann, 2001). The SORTIE model, descended from the JABOVA-FORET family, is a gap model in which trees in the gap have explicit spatial crowns (Pacala et al., 1996). The aboveground part of a single tree in SORTIE is represented as a rigid cylindrical crown, described by a species-specific radius and a crown depth around the vertical trunk, tree-plasticity patterns are not included (Pacala et al., 1996). This representation allows for the simulation of both light distribution in the canopy and tree growth in accordance with the availability of light, depending on local light heterogeneity.

Numerous individual-based stand simulators employ the zone of influence concept (Biging & Dobbertin, 1995; Bugmann, 2001; Mitchell, 1980), and crown competition is often accounted for by means of calculation of competition indices (Burton, 1993; Liu & Ashton, 1995). A zone of influence is usually defined as a circle around a tree center, where a focal tree can interact with its neighbors. This concept was used in studies of above-ground and below-ground competition (Aaltonen, 1926; Biging & Dobbertin, 1995; Casper et al., 2003). In the 19th century the term "crown ratio" was introduced to describe the ratio between d.b.h. and the average crown spread of a tree (Lane-Poole, 1936). This parameter was used as a stand characteristic reflecting the intensity of light competition in every crown class to optimize the thinning strategy, by reducing crown competition in silviculture practice (Krajicek et al., 1961; Lane-Poole, 1936). Later, the dominant-tree class was replaced by open-grown trees as the universal standard of trees which are not affected by their neighbors (Krajicek et al., 1961), and the crown area of open-grown trees was defined as a zone of influence for all trees with similar d.b.h. (Biging & Dobbertin, 1995). Comparison of zone of influences with realized dimensions yields different quantitative characteristics, the so-called "crown competition indices" (Biging & Dobbertin, 1995; Krajicek et al., 1961). Individual competition indices, calculated for a representative sample of trees from every crown class, can be averaged to produce a competition measure at the stand level. This scaling approach has several inherent limitations due to the static nature of competition indices, which restricts their usefulness in both practical silviculture and forest ecology (Burton, 1993).

The forest simulators employing the competition indices were united in a class of tree-stand models; in contrast to the crown-stand models (Mitchell, 1980), this old classification emphasizes the importance of simulating the crown and bole development. The crown-stand simulator TASS (Mitchell, 1969; 1975) employs the crown and bole as primary operating units. Crown competition in TASS is calculated as a result of the spatial intersection of the crown-profile functions of neighborhood trees. Similar crown competition algorithm was independently developed for modeling of *Eucalyptus obliqua* stands (Curtin, 1970). This modeling approach was employed in the Crown Plastic SORTIE (Strigul et al., 2008).

The next step in enhancing the realism of crown-plasticity representation is to explicitly simulate the growth of individual branches, instead of calculating a generalized crown-profile function. In 1980, K.J. Mitchell (Mitchell, 1980) included branch-stand models in the stand-model classification; however, such models were not yet developed, due to unrealistic computational resource demand. Technological progress made such models possible, and

recent branch-level models were widely used in simulations of the development of form of individual plants and the simplest, evenly distributed, even-aged single-species stands (Godin, 2000; Takenaka, 1994). Several models have been developed to simulate the effects of crown plasticity caused by independent-branch development at the stand level. The WHORL model simulates a two-dimensional forest, where an open-tree crown is represented a system of horizontal disks, simulating a crown layer (Ford, 1992). Disks and their sectors can grow and die independently depending on local light availability in the stand. As a result, a tree crown in the stand develops as an asymmetrical system of whorls stacked along a central vertical axis, representing the tree trunk. A similar crown representation, using a pyramid of independently growing discs (which are also represented by independently growing segments), was employed in the BALANCE model (Grote & Pretzsch, 2002). The LES model (section 3.2) belongs to this group of models; as the next-generation model, it simulates indigenous forests with multiple species (typical simulations are 1000 years of 1 ha plots).

Stand models such as TASS, WHORL, and BALANCE as well as SORTIE and other gap models share a similar assumption concerning tree growth: In these models, trees are assumed to grow vertically, and the zone of influence is centered at the stem base. As a result, these models do not allow for tree leaning as a mechanism of adaptive tree-morphological plasticity. An alternative approach to simulate crown plasticity was developed by K. Umeki, using the crown-vector notion proposed by S. Takiguchi (see Umeki (1995a) for details and cross references). The crown vector is the vector between the stem base position and the centroid of the projected crown area of an individual tree. The centroid's coordinates were calculated using a competition index based on a circular zone of influence (Umeki, 1995a). This approach is also employed in the Crown Plastic SORTIE and LES models to simulate changes of crown center of mass (Fig. 4) .

This brief review demonstrates that a number of individual-based forest simulators vary in their attention to the tree-morphological plasticity patterns. Ecological models, such as SORTIE, describe tree growth in great detail as it relates to fine-scale resource heterogeneity and competition, seed production, and dispersion; however, they ignore both crown competition and tree plasticity. Crown-stand simulators such as TASS provide a detailed description of crown competition and of the underlying-branch plasticity patterns; they do not include ecological patterns, however, and they ignore tree leaning. Finally, the crown-vector approach (Umeki, 1995a) represents a simple and convenient method for simulating tree-leaning patterns.

The Crown Plastic SORTIE model (Strigul et al., 2008) combines the advantages of ecological and forest management IBMs considered above, and incorporates tree plasticity patterns. In particular it includes all the ecological complexity from the SORTIE model, a crown competition algorithm similar to the TASS model, and a crown plasticity algorithm based on the crown-vector approach. This IBM is suitable for predicting prescriptions of ecological forestry concerning management of multi-species and multi-age stands. This IBM gives more realistic predictions than the previous models; in particular, it allows for the observation of canopy regularity patterns emerging as a result of canopy self-organization (Strigul et al., 2008). At the same time, in more simplified simulations without crown plasticity algorithm, crown plastic SORTIE gives the same predictions as SORTIE or TASS depending on the model parameterization employed. This model also allowed derivation of tractable macroscopic equations for forest growth called the Perfect Plasticity Approximation (Strigul et al., 2008). The next generation individual-based model, LES, is introduced below.

3.2 The LES model

An individual-based forest simulator called LES (after the Russian word for forest) simulates spatially explicit tree competition above ground for light and below ground for water and nutrients. The LES model is based on the crown plastic SORTIE model, but operates at the individual branch and root levels (Fig. 3). Trees in the LES model execute phenotypic plasticity patterns considered in section 2. In this model, trees adaptively develop their crowns and root systems to their own unique local neighborhoods.
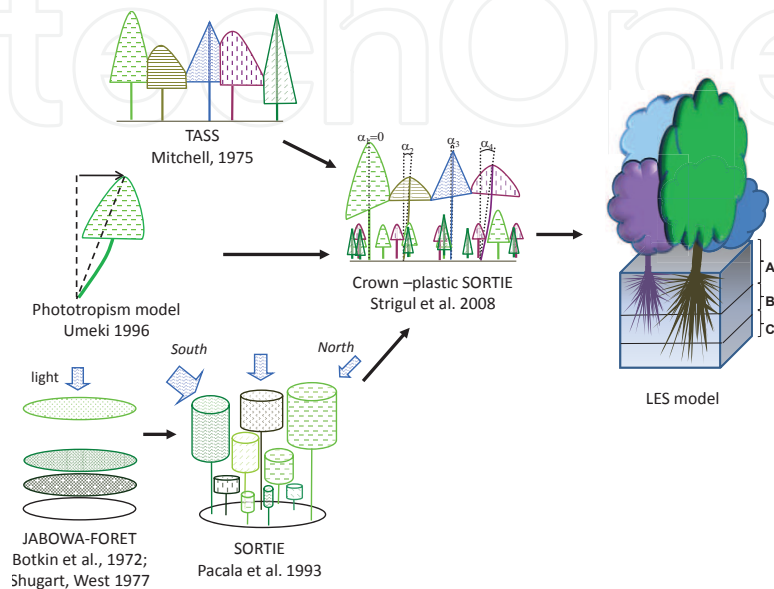
Fig. 3. Genealogy of the LES model

The most important new elements of the LES model compared to its predecessors (Fig. 3) are the following: 1) An individual tree develops a unique crown and root system within a local neighborhood to optimize spatial resource acquisition and allocation. 2) Vertical forest stratification emerges from the branch level competition. The model simulates the development of canopy, midstory and understory levels, allowing for tree classification as dominant, codominant, intermediate and suppressed trees. 3) Tree root systems are described by individual roots, and a vertical soil stratification emerges from individual root competition in three distinct soil horizons.

With respect to crown competition the Crown Plastic SORTIE model (Strigul et al., 2008) includes two essential elements: 1) Crown parametrization and competition algorithm similar to the TASS model, and 2) phototropism algorithm similar to one developed by Umeki (Umeki, 1995a). This model assumes that every tree has a species-specific potential crown shape, which is rotation-symmetrical about the vertical axis through the center of the crown. The realized tree crown is part of the potential crown determined by the spatial tessellation algorithm (Strigul et al., 2008). The advantage of this crown representation is that it leads to the computationally simple and fast algorithm as a horizontal cross section of the potential crown at any height is a circle. However, the major disadvantage is that the Crown Plastic SORTIE assumes the existence of a symmetrical potential crown shape for any tree growing within the forest stand. In the LES model this assumption is relaxed, and the individual crown shape develops as the result of adaptive tree growth within the unique local neighborhood. The new crown algorithm introduced in the LES model (Fig. 4) results in the development of a more realistic canopy than in the Crown Plastic SORTIE model.
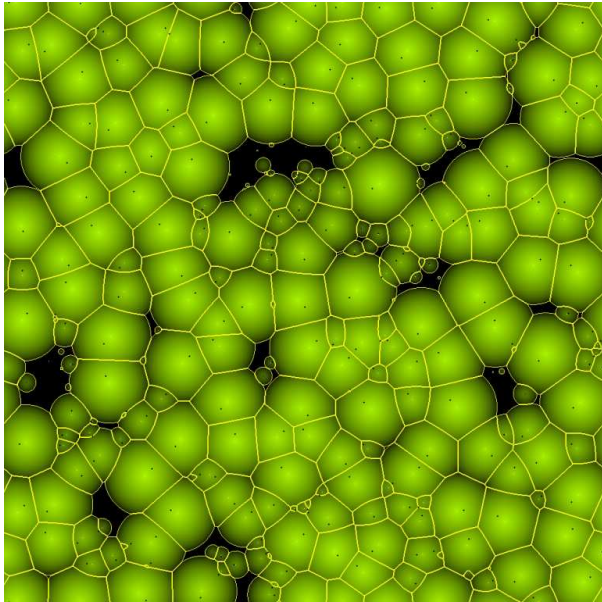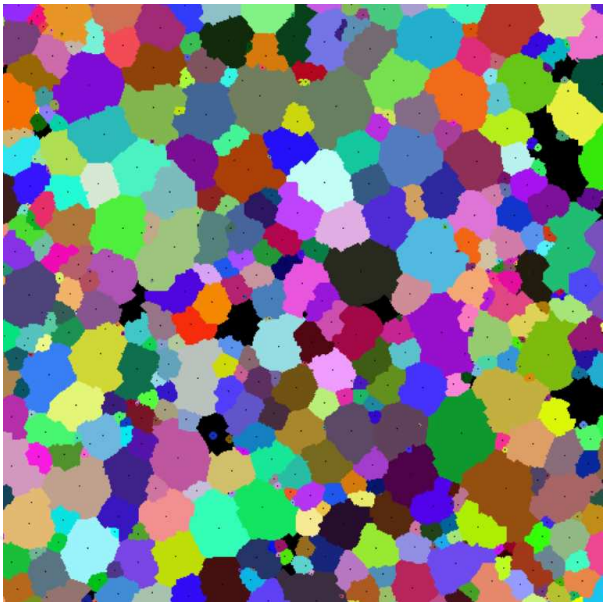
(a) Canopy simulated with the Crown Plastic SORTIE model.
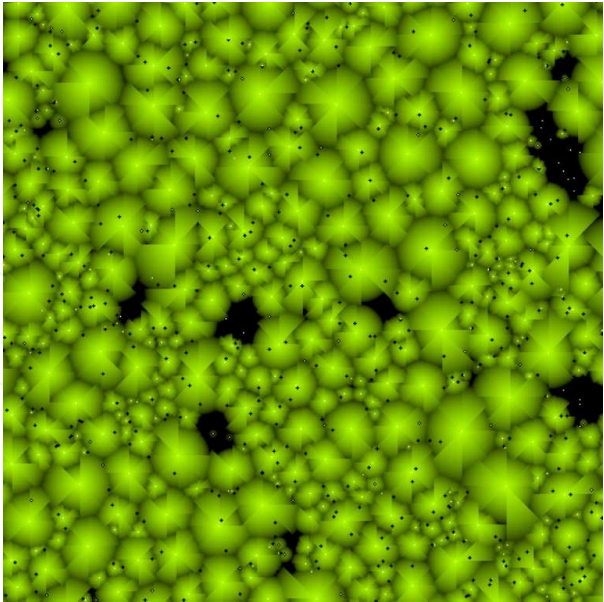
(b) Canopy simulated with the LES model.
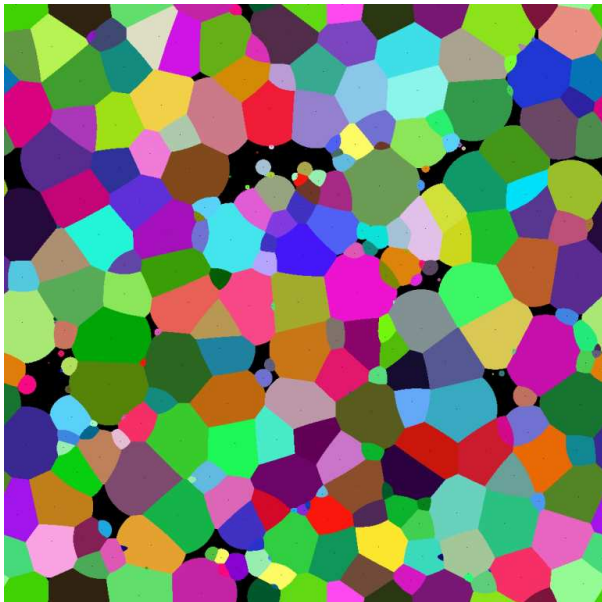
(c) the crown shape projection on the ground in the Crown Plastic SORTIE simulations.

(d) the crown shape projection on the ground in LES model simulations.

Fig. 4. Forest canopy simulations in the Crown Plastic SORTIE model (Strigul et al., 2008) and the LES model. In the Crown Plastic SORTIE model (a and c) a realized tree crown is determined as a part of the symmetrical potential crown by the tessellation algorithm (Strigul et al., 2008). In the LES model an individual tree crown develops as the result of adaptive spatial crown development within the unique local neighborhood. Tree crown develops on three hierarchical levels: leave and small branches, large branches (represented as independent spatial sectors) and crown level, represented by the crown center of mass. The figure demonstrates two different canopy visualizations: height-density plots (a and b) and crown ground projection plots (c and d) of canopy trees in a simulated White Pine forest stand (0.25 ha) 200 years after a major disturbance. The brightness level in figures a and b indicates the crown height at every point.

The LES model simulates a tree crown as a hierarchical three-dimensional spatial structure that develops and changes in response to environmental conditions on multiple levels. The LES model incorporates adaptive and random changes on three structural levels: 1) small branch and leaf level, 2) large branch level, 3) crown level. The first level of the crown organization in the LES model corresponds to leaves and small branch level, where every point represents an area of approximately 10 cm^2. Every such crown unit is represented as a point on a two-dimensional grid with the height of this crown component as a parameter. The canopy competition occurs independently at every point, where the highest crown wins the spatial competition. The second level of crown organization in the LES model is the level of large branches represented as independent crown sectors. Every sector is characterized by its width, the height of the lowest leaves and the leave distribution profile within the sector. These characteristics of every individual crown sector are determined by the results of spatial competition in the given neighborhood. The model can simulate crowns with 2^n sectors; most of the simulations are conducted with 8 crown sectors. The largest level of crown organization is the crown level determined by the center of the crown (center of mass); its position is determined by the algorithm of phototropism and crown leaning developed in the Crown Plastic SORTIE model (Strigul et al., 2008).

(a) Three dimensional root competition in the LES model.

(b) Root systems in the A soil horizon. 40 years after a major disturbance.
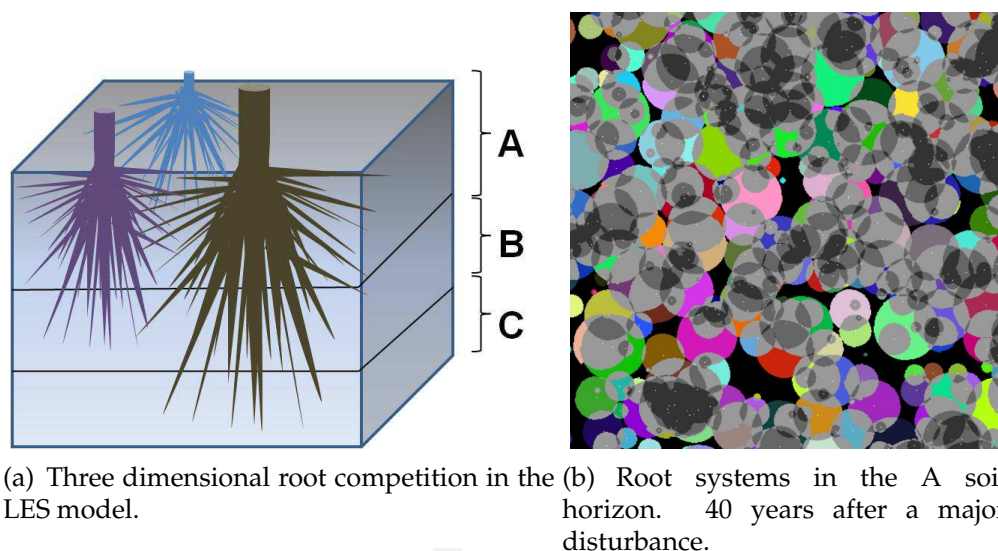
Fig. 5. Simulation of underground root competition in the LES model. A tree root system develops in three soil horizons: top (A), intermediate (B) and low (C). The soil within each horizon is represented as a collection of disjoint spatial units (cuboids), where each soil unit has its own available water content and can be occupied by roots of one or several trees competing for water and nutrients. An individual root system develops independently in different spatial directions corresponding to large roots (simulated as spatial sectors). Trees optimize water uptake by investing available resources in growth of the most efficient root sectors in different soil horizons.

The Crown Plastic SORTIE and all its ancestors focused entirely on the tree competition for light, and ignored below-ground competition for water and nutrients. In the LES model trees have spatial three-dimensional root systems and compete for water and nutrients (Fig. 5(a), 5(b)). Therefore tree growth and resource allocation can be simulated depending on multiple resource limitations (Fig. 6), and, in particular, carbon and water balance are considered at the tree level. The major patterns of belowground tree competition in the LES model are: 1)

The three independent soil horizons (A, B and C on Fig. 5(a)), 2) The spatially heterogeneous water/nutrient distribution within horizons, 3) Several trees can occupy every unit of soil, 4) Directional root growth within each horizon, 5) Individual trees optimize root system growth in three dimensions according to competition constraints and resource availability.
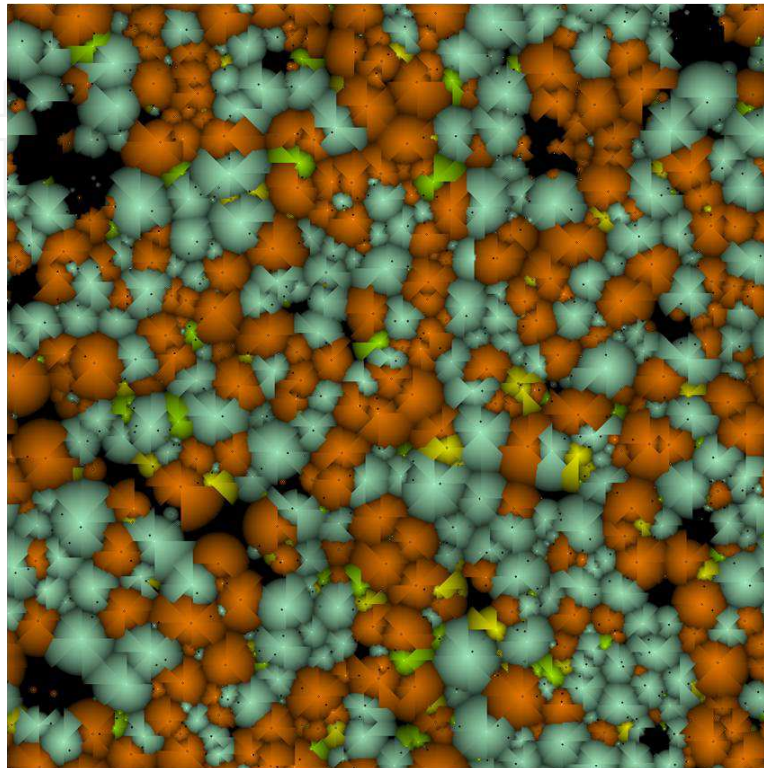

Fig. 6. Canopy level in the LES model simulation of stand development over 200 years, where trees compete for light and water simultaneously. Two different tree species that are colored grey and brown when trees are water-limited, and green and yellow when trees are light-limited, respectively. Most of the canopy trees are water-limited; only several trees with insufficient crowns are light-limited.

3.3 The Perfect Plasticity Approximation (PPA) model

Forest simulation models are effective tools in scaling individual-level spatio-temporal processes to the stand level because they are able to simultaneously incorporate tree ecophysiological traits such as carbon allocation, and capture tree level disturbances and gap dynamics. Individual-based models can also be applied to simulate vegetation dynamics at the landscape level using GIS-based inputs. The major disadvantage of forest individual-based models is that these spatial stochastic processes are not analytically tractable, so their general properties and sensitivities to the choice of parameters and functional forms are uncertain. However, analytically tractable approximations of individual based forest simulators can be developed. In particular, the Perfect Plasticity Approximation (PPA, Strigul et al. (2008)) is a recently developed model predicting the stand-level forest dynamics by scaling up individual-level processes. The PPA offers good predictions for 1) stand-level attributes, such as basal area, tree density, and size distributions; 2) biomass dynamics and self-thinning; and 3) ecological patterns, such as succession, invasion, and coexistence. The model includes a system of von Foerster partial differential equations and the PPA equation.

Unlike the individual-based simulator, the PPA model is both analytically tractable and computationally simple. Initially the model was developed as an approximation of the crown plastic SORTIE model (Strigul et al., 2008), but it was also demonstrated that the PPA model captures the dynamics of the temporary forests. Purves at al. (Purves et al., 2008) estimated the parameters of the PPA model by using the data collected by the Forest Inventory and Analysis (FIA) Program of the U.S. Forest Service (FIA data) for the US Lake states (Michigan, Wisconsin, and Minnesota). It was demonstrated that the PPA model, applied even in its simplest form, carefully predicts forest dynamics and succession on different soil types.

The PPA model is a cohort model assuming time is discrete and is the following boundary value problem if the time is measured continuously (Strigul et al., 2008). The continuous version of the PPA model for m tree species consists of m von Foerster equations (1) with initial $N_i(s, 0)$ and boundary conditions (2) for every species $i = 1, \ldots, m$ connected by the integral PPA equation (3) for the threshold canopy size $s^*(t)$:

$$\frac{\partial N_i(s, t)}{\partial t} = - \underbrace{\frac{\partial \left(G_i(s, s^*(t), t) N_i(s, t) \right)}{\partial s}}_{growth} - \underbrace{\mu_i(s, s^*(t), t) N_i(s, t)}_{mortality}, \tag{1}$$

$$N_i(s_{i,0}, t) = \int_{s_{i,0}}^{\infty} N_i(s, t) F_i(s, s^*(t), t) ds / G_i(s_{i,0}, s^*(t), t), \tag{2}$$

$$1 = \sum_{i=1}^{m} \int_{s^*(t)}^{\infty} N_i(s, t) A_i(s^*(t), s) ds, \tag{3}$$

where i indicates one of m tree species, s is the size of the tree that can be either tree height or dbh connected with height by a species specific allometric equation, $N_i(s, t)$ is the mean density of individuals of species i of size s at time t, $G_i(s, t)$ is the growth rate of these individuals i.e., $ds/dt = G(s, s^*(t), t)$), $\mu_i(s, s^*(t), t)$ is their death rate, $F_i(s, s^*(t), t)$ is their fecundity, $A_i(s^*(t), s)$ is the crown area function that gives the area of the crown at s, and $s_{i,0}$ is the size of a newborn of the ith species. Growth, death and fecundity functions depend on time t and tree size s as well as the canopy threshold level $s^*(t)$.

Strigul et al. (Strigul et al., 2008) considered transient and stationary regimes of tree monocultures as well as simple invasion and coexistence problems. The model was parameterized for different soil types so the patch (stand) dynamics at different soil and forest types types can be considered separately.

4. The Matreshka model: hierarchical scaling of forest dynamics to the landscape level.

This section introduces a modeling framework, called Matreshka (after the Russian nesting doll), for the scaling of vegetation dynamics from the individual level to the landscape level through the ecosystem hierarchical structure (Figure 7, see also Strigul et al. (2012)). The Matreshka model is a particular realization of the hierarchical patch dynamics concept (Levin & Paine, 1974; Wu & Loucks, 1996) in application to forested ecosystems. The model (Fig. 7) represents forest dynamics at the landscape level as an interference of separated processes occurring at different spatial and temporal scales: 1) within forest stands dynamics caused by individual-level disturbances, and 2) dynamics of the mosaic of forest stands caused by large disturbances. The Matreshka model can be presented as a continuous or a discrete model, where partial differential and integral equations and Markov chains are employed,
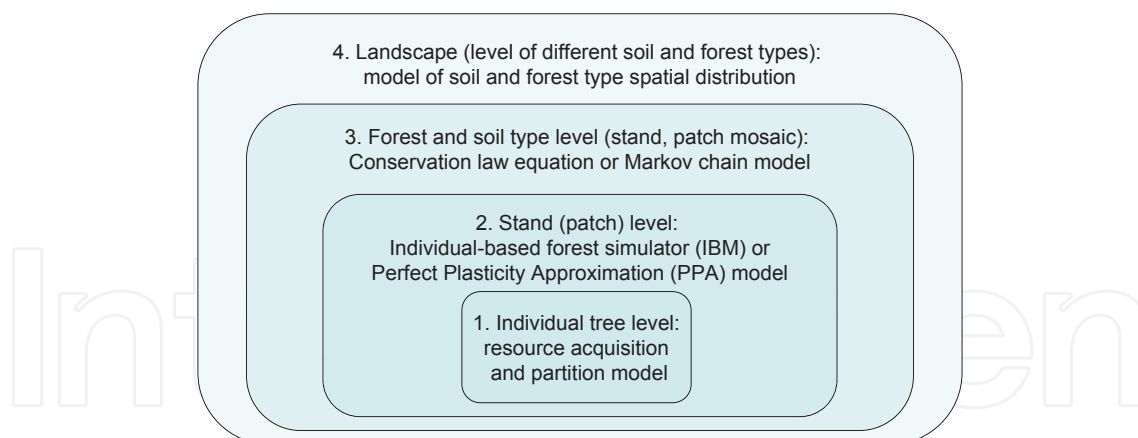
Fig. 7. The Matreshka framework for hierarchical scaling of vegetation dynamics to the landscape level

respectively. The highest hierarchical level is the landscape level comprising a mosaic of different soil and forest types. The vegetation dynamics at this level are the composition of vegetation dynamics of different forest types. The forest and soil type level consists of the mosaic of forest patches that are in different successional stages. In this model, forest patches are considered as spatial units of a considerably large size (0.5 - 1 hectare). A broad discussion of the model assumptions can be found in a recent paper (Strigul et al., 2012) focusing on the dynamics of forest stands (level 3 on Fig. 7). The Matreshka employs previously developed models for the processes at smaller scales. In particular, tree dynamics within the forest stands can be modeled by an individual-based forest growth model (for example, SORTIE, Crown Plastic SORTIE or LES models) or by forest growth macroscopic equations, specifically, the Perfect Plasticity Approximation model (PPA). The individual tree level model captures growth, mortality, and reproduction of individual trees depending on tree size, light and nutrient availability, soil type, and other factors. Several empirically determined parameters approximate these individual-level processes in the SORTIE and PPA frameworks (Pacala et al., 1996; Strigul et al., 2008).

At the next step of scaling, age-structured dynamics of forest stands (patches) on the given soil type can be described by the conservation law following Levin and Paine (Levin & Paine, 1974) in the continuous case:

$$\frac{\partial n(t,a,\xi)}{\partial t} = -\frac{\partial n(t,a,\xi)}{\partial a} - \frac{\partial g(t,a,\xi)\, n(t,a,\xi)}{\partial \xi} - \mu(t,a,\xi)\, n(t,a,\xi), \tag{4}$$

where, $n(t,a,\xi)$, $g(t,a,\xi)$ and $\mu(t,a,\xi)$ are density, mean growth rate and extinction rate of a stand of state a and size ξ at time t, correspondingly. The initial stand distribution $n(0,a,\xi)$ and the "birth rate" of new stands should be specified to simulate given forested ecosystem.

The original model operates with two variables (patch age, a, and size, ξ), but it has been indicated (Levin & Paine (1974) p. 2745) that age is just one of the possible "physiological" variables. In this chapter, we consider a special case of equation (4), where the forest patches are fixed in size, so the rate of patch growth is zero $g(t,a,\xi) = 0$. Variable a is considered as a successional stage of forest stand, and is discussed in another paper (Strigul et al., 2012). This formulation of the Matreshka model (equations 1-4) is analytically tractable in special cases, though the general analysis is a significant challenge. In particular, in the following example we consider the stationary distribution of tree monoculture stands.

In the discrete case Strigul et al. (Strigul et al., 2012) proposed a discrete time Markov chain model for stand (patch) dynamics that can be easily generalized to a continuous time framework by taking random times between transitions. However, the discrete modeling approach has certain advantages such as that the transition of stands between stages can be explicitly defined, the probability matrix is easy to interpret and estimate using forest inventory data. In the general Markov chain model for the stand transition (Strigul et al., 2012), the states in the Markov chain are represented by stand successional stages $\{1, 2, \ldots, m\}$ characterizing the forest stand development up to a certain maturity stage m. In certain applications, such as forest fire models, the successional stage is characterized by the absolute stand age, i.e., the time since the latest major fire disturbance. However, in general, the choice of the parameter characterizing stand successional stage can be a challenging problem. The model for development of one stand (patch) may be represented using a graph as in Figure 8 and is described using a general transition probability matrix (5):

$$
P = \begin{pmatrix}
r_1 & p_1 & 0 & 0 & \ldots & 0 & 0 \\
q_{2,1} & r_2 & p_2 & 0 & \ldots & 0 & 0 \\
q_{3,1} & q_{3,2} & r_3 & p_3 & \ldots & 0 & 0 \\
\vdots & & & \ddots & \ddots & & \\
\vdots & & & & \ddots & \ddots & \\
q_{m-1,1} & q_{m-1,2} & q_{m-1,3} & q_{m-1,4} & \cdots & r_{m-1} & p_{m-1} \\
q_{m,1} & q_{m,2} & q_{m,3} & q_{m,4} & \cdots & q_{m,m-1} & r_m
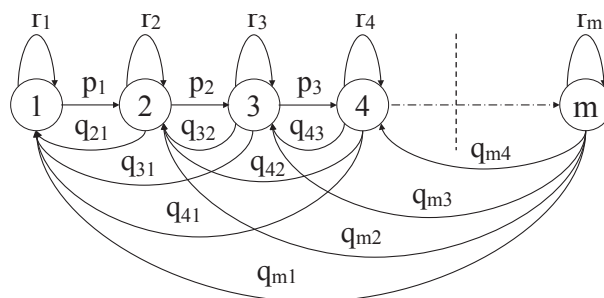\end{pmatrix}
\tag{5}
$$

Fig. 8. A graph of the complete stage dynamics model of forest stands (after Strigul et al. (2012)).

The model assumes that the patch (forest stand) is observed frequently enough relative to the succession process so that the forest does not grow through two consecutive successional states. Each time the forest stand moves to the next stage with probability p_i or stays at the same stage with probability r_i (due to some minor forest disturbances or a small interval between forest inventories). The $\{q_{ij}\}_{i \in \{2,\ldots,m\}, j \in \{1,\ldots,m-1\}}$ probabilities describe disturbances affecting stand succession. The disturbances include disaster events which completely destroy forest stands ($q_{x,1}$, $x = 2, \ldots, m$) or smaller-scale events which change the stand successional stage to one of the previous stages with certain probabilities ($q_{h,k}$, $h > k > 1$). These disturbances determine the development of forest as a mosaic of patches (stands). The model makes no distinction or explanation between the causes of the disturbances leading to the successional stage, in particular, both silvicultural operations such as forest harvesting or natural disturbances would lead to larger $q_{i,j}$ probabilities (Strigul et al., 2012).

The Matreshka model is considered as a first step in development of an analytically tractable model capable of capturing the forest dynamics on multiple scales. However, the PPA (1-3)

model and the forest stand model (7) as well as its discrete counterparts such as Markov chain models (8), are only partially analytically tractable. In particular, the stationary states of these models and their stability can be relatively easily investigated, while the transient dynamics is a challenging problem. Therefore, we are still far away from complete mathematical theory of multiscale forest dynamics.

The key element for the Matreshka model is to simulate forest dynamics as a patch-mosaic phenomenon at two distinct hierarchical scales: at the individual level and the stand level (7). In forest ecology the two focal scales (i.e. individual and stand levels) have been broadly discussed with respect to forest dynamics and disturbance regimes (Bragg et al., 2004; Strigul et al., 2012). Patch-mosaic dynamics of larger forest units (stands) have also been considered in different studies, such as in forest fire models, forest disease models, and anthropogenic disturbance modeling (Bragg et al., 2004; Forman, 1995; Wu & Loucks, 1996). In the Matreshka model, we use the PPA model to scale up gap dynamics to the stand level and consider forest patches as much large spatial units (about 0.5-1 ha, see (Strigul et al., 2012) for more details).
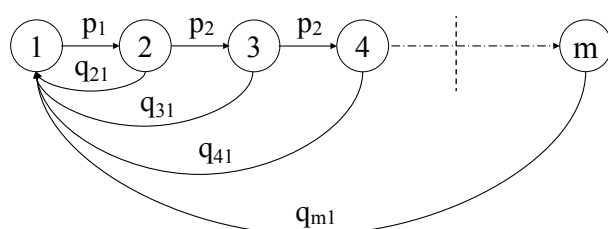

Fig. 9. A graph for a simplified forest stand model. The Birth and Disaster Markov chain.

4.1 Fire disturbance model: a case study

In this example, an analytically tractable case of the Matreshka model is considered. The simple case of the PPA model-the flat-top model-is employed to describe a tree monoculture stand (Strigul et al., 2008). The flat-top model was parameterized and validated for the Lake states (Purves et al., 2008). This model is a special case of the PPA model (equations 1-3) where tree growth and mortality are characterized by several species-specific constant parameters such as understory and overstory rates of growth as well as mortality and fecundity parameters. Using these simplest possible functional forms makes the model analytically tractable (Strigul et al., 2008). In particular, there exists a unique stable stationary state of a flat-top monoculture stand, and stationary age and size distributions of trees within the stand can be calculated. The transient dynamics are less tractable; however, the self-thinning exponents were analyzed analytically (Strigul et al., 2008), and a good approximation of the total length of transient period (t^*) for the case of the invasion into an empty habitat was derived (unpublished results). The length of the transient period curve corresponding to the stand development, starting from the invasion into an empty habitat until the stationary state, may be approximated by a piecewise linear model:

$$x(t) = \begin{cases} \alpha\, t, \ t \leq t^*, \\ x^*, \ t > t^* \end{cases} \tag{6}$$

where $x(t)$ is a stand characteristic (such as biomass or cumulative basal area), x^* - stationary value of the quantity $x(t)$, t^* is the length of the transient period, and a parameter α is x^*/t^*, so it can be determined if the values x^* and t^* are known. This piecewise-linear approximation is commonly used in microbiology to approximate sigmoidal growth in microbial cultures. Sigmoidal growth models, for example, Gompertz and logistic curves, are often used to

describe growth of stands and individual trees as well as microbial cultures (Dette et al., 2005; Yoshimoto, 2001).
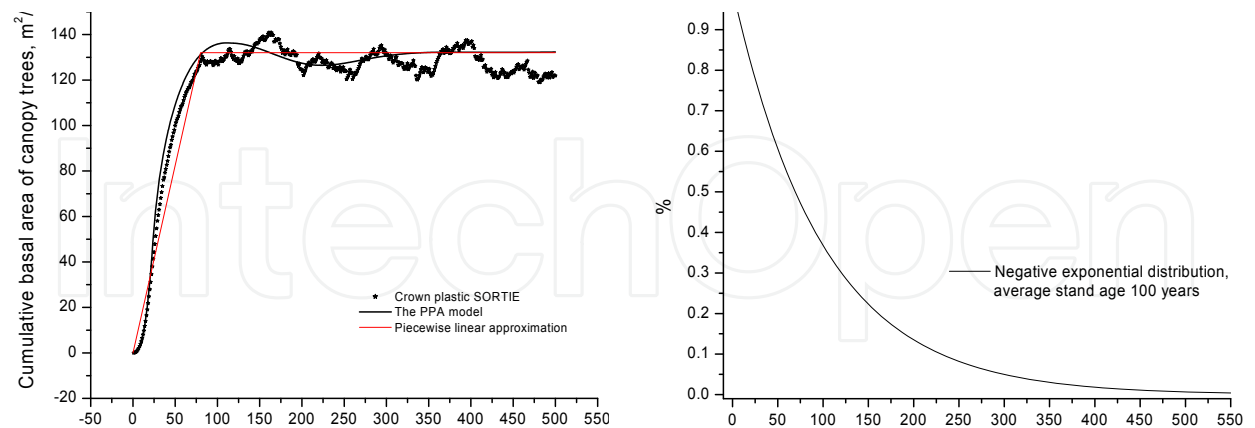
(a) Dynamics of the cumulative basal area of the hypothetical stand of white pine simulated by the crown plastic SORTIE model (black points) and the PPA model (black line) (see Strigul et al. (2008) for the details and parameter values), the red line is a piecewise linear approximation.

(b) The stationary stand age distribution of the mosaic of forest patches represented by the negative exponential distribution in the forest fire model (after Van Wagner (1978)).
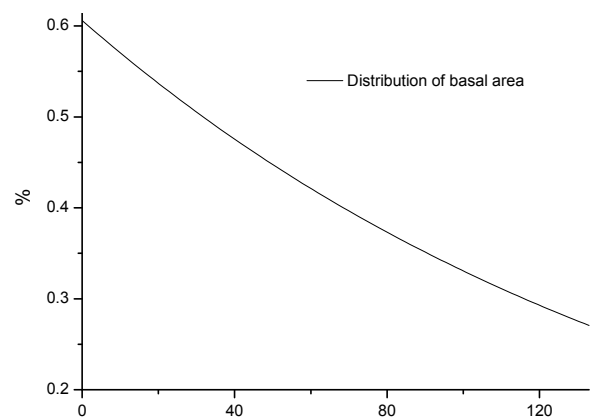
(c) The stationary distribution of stand basal area of the mosaic of forest patches.

Fig. 10. An example of the fire disturbance model for a tree monoculture.

We consider a special case of equation (4) to describe the stand level dynamics of tree monoculture. In particular, we assume that the stands are fixed in size, i.e. $g(t, a, \xi) = 0$ and have constant extinction (disaster) rate μ, to obtain the following model:

$$\frac{\partial n(t,a)}{\partial t} = -\frac{\partial n(t,a)}{\partial a} - \mu\, n(t,a). \tag{7}$$

This model describes the patch-mosaic pattern of stands, given some initial stand distribution $n(0, a)$ and assuming that new stands emerge in place of extinct stands. The discrete version of equation (7) is a birth-disaster Markov chain with constant parameters p and q (Fig. 9). This model, with the successional stage a considered as stand age, is mathematically equivalent to the classical forest fire model developed by Van Wagner (Van Wagner, 1978). It is a simple

mathematical exercise to show that the model (7) has a stable stationary distribution described by a negative exponential law which after standardization can be presented as the negative exponential distribution with the following probability density function:

$$f(a, \mu) = \begin{cases} \mu e^{-\mu a} & a \geq 0, \\ 0, & a < 0. \end{cases} \tag{8}$$

The negative exponential distribution as well as its discrete version - the geometric distribution are employed in forest fire models to describe stationary age distributions of forest stands (Johnson & Gutsell, 1994; Van Wagner, 1978).

Using the Matreshka framework, we can now scale up the predictions of the PPA model to the level of mosaic of forest stands. We can invert equation (6) as a function of $t(x)$ on an interval $[0, t^*]$ and there are infinitely many values of t corresponding to the value x^*. Substituting this result in equation (8) we obtain the stationary probability distribution of the quantity x:

$$f(x, \mu, \alpha) = \begin{cases} \mu\, e^{-\frac{\mu x}{\alpha}} & 0 \leq x < x^*, \\ \left(1 - \int_0^{x^*} \frac{\mu}{\alpha}\, e^{-\frac{\mu x}{\alpha}}\, dx\right) \delta(x - x^*), & x = x^*, \\ 0, & x < 0 \text{ and } x > x^*, \end{cases} \tag{9}$$

where $\delta(x)$ is the Dirac delta function that accounts for all the stands which are in the stationary state. In the discrete case, the geometric distribution may be considered instead of distribution (8). In that case, the transformed distribution corresponding to (9) will have only a finite number of values. The coefficient for the resulting Dirac delta function in (9) will be the last value corresponding to x^* in this distribution.

As an illustrative example, we consider a stand of white pine (*Pinus strobus*) simulated by the crown plastic SORTIE and the corresponding PPA model. Figure 10(a) presents the simulation results (reproduced with permission from (Strigul et al., 2008)). The model functional forms and parameter values are available in the latter reference. In this example, the parameter $x(t)$ is a stand cumulative basal area; however, biomass, average canopy height etc. may be employed instead. Figure 10(b) illustrates the negative exponential distribution of stand ages corresponding to the stationary state of equation (7) with $\mu = 0.01$. This parameter value corresponds to an example considered by Van Wagner in his classical work on forest fire modeling (Van Wagner, 1978). Figure 10(c) presents the distribution (9), where 44.93% of all stands have the stationary state basal area $x^* = 132\, m^2/ha$. Note that the shape of the distribution (9) is determined by the values of μ, x^*, and t^*. Therefore, the stationary distribution (9) predicted by this simple modification of the Matreshka model may be observed and verified subject to data availability.

This example is based on the tree monoculture model (Strigul et al., 2008) and therefore is of limited practical value for the SFM of indigenous multispecies forests. However, even this simplified model can be implemented directly for certain forest types that are naturally dominated by one tree species. One particular example is the longleaf pine (*Pinus palustris* Mill.) forest that has historically dominated the Southeastern United States. This natural monoculture ecosystem was supported by forest fires, as the longleaf pine is fire resistant. Development of its competitors, such as loblolly (*Pinus taeda*) and slash (*Pinus elliottii*) pines, has been limited by frequent forest fires. Over the last 150 years the landscape has changed radically due to overexploitation and fire suppression. Intensive longleaf pine forest restoration projects at the Southeastern U.S. are currently on-going within the SFM framework (www.longleafalliance.org).

This example demonstrates the potential advantages of using the multiple-scale modeling for SFM applications. The Van Wagner fire-disturbance model operates with the stand age after a major disturbance (Van Wagner, 1978). Therefore, the forest management plans within this model should be based on the fire-disturbance history. In practice, the exact fire history is often hard to determine. Forest surveys, such as USDA FIA data and Canadian forest service data, determine the stand age empirically as an average age of canopy trees. This parameter is unfortunately not very reliable for modeling purposes (Strigul et al., 2012). The Matreshka model allows one to develop the forest management plans using forest stand stratification with respect to the stand successional stage, basal area, or stand biomass. The stand biomass or basal area can be easily calculated using available survey data (Strigul et al., 2012) and the forest management plan can be designed based on these stand characteristics. This makes the model suitable for the needs of criterion 1.1 (Ecosystem diversity) of the Montreal process.

4.2 Application of the Matreshka model to criterion 5 of the Montreal process

The Matreshka model is developed for ecological forestry and SFM applications. Specifically, it allows one to incorporate natural and anthropogenic disturbances occurring at different scales, ranging from individual trees to stands to predict forest growth at the landscape level. To address criteria 2 and 5 of the Montreal process, the model can naturally incorporate effects of climate change on individual tree growth through modification of either the forest individual-based model or the PPA model. Changes of the natural disturbance regime due to climatic factors can be incorporated by modification of tree mortality functions or by changing elements and structure of the transition matrix 5 (for stand-level disturbances). Similarly, changes in forest policy, silvicultural practices, and anthropogenic disturbances can also be incorporated in the model through modification of tree mortality functions and the transition matrix 5. While the Matreshka model is formulated as a non-spatial model at the stand level, the model can also be presented in a spatially explicit form by using GIS-based simulations of forest stands at the landscape level. This can be essential if the forest stewardship in the focal area varies due to different landowner policies.
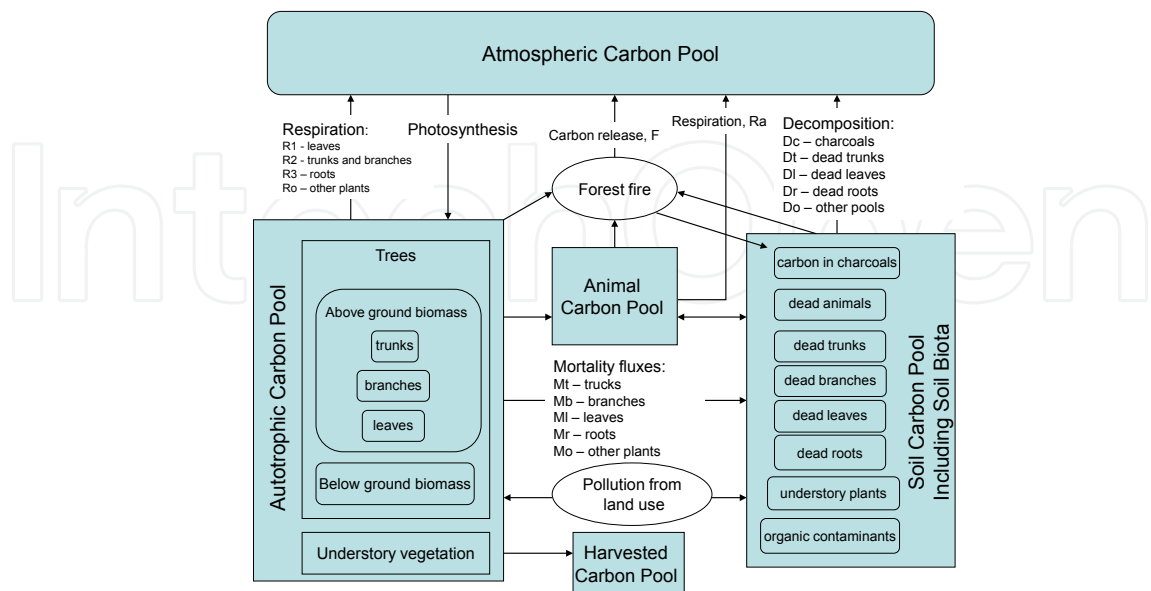

Fig. 11. The framework for modeling of forest carbon footprint for the SFM applications. The Matreshka model is used for the modeling of Autotrophic and Soil Carbon Pools.

Current on-going research is focused on the application of the Matreshka model to the carbon cycle modeling of temperate forests in the North-Eastern Part of the USA and Quebec in agrement with criterion 5 of the Montreal process "Maintenance of forest contribution to global carbon cycles". The carbon footprint of forest ecosystems is determined by the dynamics of carbon sequestration and release, and can be affected by harvesting and other anthropogenic activities. In this project, the Matreshka model is used to predict the forest carbon cycle according to a conceptual model presented in Figure 11. Most of the carbon influx into the ecosystem is derived from photosynthetic assimilation of atmospheric CO_2 by the autotrophs (overstory trees, understory trees, shrubs, and groundcover vegetation) that determine the gross primary productivity (GPP). The major effluxes of carbon in the atmosphere occur as the result of autotrophic respiration (which is defined as the sum of maintenance respiration and growth respiration), heterotrophic respiration, and the processes of physical decomposition of organic matter, such as fire. Carbon is also removed from a forest ecosystem by wood harvesting. The typical parameters of interest in calculating carbon footprints are the net primary production (NPP, defined as GPP minus autotrophic respiration), and the net ecosystem production (NEP). The NEP is determined as the net exchange of CO_2 between the atmosphere and ecosystem, which is measured on an annual basis, and equal to the NPP minus heterotrophic respiration. During recent decades, carbon fluxes presented in Figure 11 were evaluated, however, the current models operate with the carbon balance at the macroscopic level using average estimates of the carbon pools and fluxes. In this project, the key element for predicting forest carbon cycle is the Matreshka model. This model provides a scaling of carbon balance from an individual tree level to the stand level, and simulates the autotrophic carbon pool (Fig. 11). Therefore, the carbon balance model incorporating the Matreshka model scales up the effects of the silvicultural practices and other anthropogenic activities from the individual tree-based level to the ecosystem level, and can predict changes in the forest structure and carbon dynamics at different time horizons.

5. Conclusion

In this chapter the framework of complex adaptive systems is employed to address the basic challenge of the ecological forestry and SFM, i.e., to understand and predict how natural and anthropogenic disturbances occurring at different scales propagate through the forested ecosystems and affect forest structure and dynamics. This framework naturally combines experimental and theoretical approaches. This framework consists of three major components: 1) the development of individual-based models (IBMs) to simulate multiple scales processes in complex systems, and their parameterization with experimental data (in particular, by using USDA forest inventory data, FIA); 2) the development of different scaling methods that approximate individual-based processes; and 3) validation with real data and practical applications. The first component involves mostly computer simulations of what are, in general, analytically-intractable stochastic processes. Forest growth IBM can serve as an intermediate research step in the derivation of macroscopic equations (i.e., tractable analytic models approximating this stochastic process), and, as an independent research tool, to simulate forest carbon balance, stand dynamics, natural disturbances (such as disease outbreaks), and the outcomes of silvicultural prescriptions. Scaling methods may allow models to be reduced to analytically tractable objects, macroscopic equations-such as stochastic and deterministic dynamical systems-which are both more robust in their predictions and, also, computationally simpler. Recently developed models including the Crown Plastic SORTIE, LES, and PPA have been developed within this research framework

to address the scaling of vegetation dynamics from the individual to the stand level. All these models employ individual tree plasticity as a crucial factor for canopy development and forest self-organization within the stand level. The Matreshka model generalizes these models operating on the individual level for scaling of vegetation dynamics to the landscape level using the hierarchical patch dynamics concept. It is anticipated that these new modeling tools will be employed for the SFM of indigenous forests. Practical applications of the developed modeling approach address criteria 2 and 5 of the Montreal process. The ongoing research focuses on the modeling of the temperate forest carbon cycle in the North-Eastern USA and Quebec. The Matreshka modeling framework can help natural resource managers to understand how changes in forest management practices can affect the forest carbon footprint, and to manage the key ecosystem processes that control carbon and nutrient dynamics in a forest ecosystem.

6. Acknowledgement

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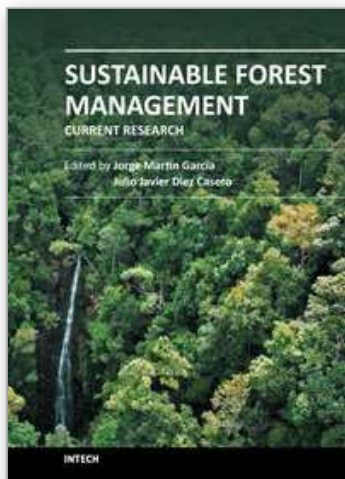
Sustainable Forest Management - Current Research

Edited by Dr. Julio J. Diez

Sustainable forest management (SFM) is not a new concept. However, its popularity has increased in the last few decades because of public concern about the dramatic decrease in forest resources. The implementation of SFM is generally achieved using criteria and indicators (C&I) and several countries have established their own sets of C&I. This book summarises some of the recent research carried out to test the current indicators, to search for new indicators and to develop new decision-making tools. The book collects original research studies on carbon and forest resources, forest health, biodiversity and productive, protective and socioeconomic functions. These studies should shed light on the current research carried out to provide forest managers with useful tools for choosing between different management strategies or improving indicators of SFM.

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