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Adapting GePSi (Generic Plant Simulator) for modeling studies in the Jasper Ridge CO_2 project[1]

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Abstract

In order to conduct modeling studies on the effects of elevated atmospheric carbon dioxide concentration ([CO_2]) on plant and ecosystem processes at the Jasper Ridge grassland in northern California, the generic plant simulator (GePSi) (Chen, J.-L. and Reynolds, J.F., 1997. Ecol. Model., 94: 53–66), is modified to simulate grass dynamics. This modification was attempted by the authors of this paper, who had no prior experience with the model. Prior to this project, GePSi, which is implemented in the object-oriented programming (OOP) language, C++, had only been used to model trees and woody shrubs. This exercise addressed several of the concepts presented in this volume concerning the purported benefits of genericness, modularity, and OOP in plant modeling. The objective of this paper is to briefly summarize the extent to which these benefits were realized and some of the problems encountered. Our evaluation is presented in terms of: (1) design considerations, including the importance of how the modules in GePSi were defined; and (2) the implementation phase, which critiques the use of OOP for facilitating the transfer of the model. This study suggests that generic, modular models such as GePSi will facilitate the interactions of model developers and users and reduce duplication of effort in model development.

Keywords: Grassland; Object-oriented programing; Modular; Generic; Validation

1. Introduction

Increasing atmospheric carbon dioxide concentration ([CO_2]) is a global phenomenon that has the potential to significantly affect both natural and agricultural ecosystems. It is a major challenge for both experimentalists and modelers to predict large-scale, long-term ecosystem responses to elevated [CO_2] (Dahlman, 1985; Reynolds et al., 1996; Strain and Thomas, 1992). Present experimental techniques, however, only allow us to make small-scale ecosystem measurements, mainly at the plant level (Schulze and Mooney, 1993). Measurements at small scales indicate that re-

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sponses of plants and ecosystems to elevated [CO_2] are extremely variable (Koch and Mooney, 1996; Poorter, 1993), making it difficult to extrapolate from small-scale measurements to the prediction of large-scale responses.

The Jasper Ridge CO_2 project in northern California was designed to explore long-term ecosystem–scale responses to elevated [CO_2] by utilizing a number of distinctive features of the serpentine and sandstone grasslands of Jasper Ridge (Field et al., 1996). The soil carbon content in the grasslands, for example, is relatively low, ranging from 3 to 9 kg m^{-2} or 10–20 times annual net primary productivity. This gives us a reasonable probability of detecting a modest change in carbon storage after only a few years of exposing swards to elevated [CO_2] in ca. 0.6 m^3 open top chambers. Also, the plants are small in stature and mostly annuals, completing all stages of their life cycles within 1 year, which gives us the opportunity to study [CO_2] effects on both vegetative and reproductive growth in a single growing season.

Modeling studies are a critical component of the Jasper Ridge CO_2 project. Modeling is being used to elucidate [CO_2]-induced changes in belowground carbon and nitrogen processes, ecosystem hydrological cycles, and species competition. Modeling studies can also help bridge the gap between the discrete measurements of several ecosystem processes and can provide an integrated view of whole-system dynamics. To date, models have been used to understand and interpret photosynthetic acclimation, root/shoot ratio adjustments (Luo et al., 1994), and relationships between leaf photosynthesis and ecosystem productivity in elevated [CO_2] (Luo et al., 1997).

In order to conduct modeling studies of the effects of elevated [CO_2] on plant and ecosystem processes at Jasper Ridge, we recently attempted to adapt the generic plant simulator, GePSi (Chen and Reynolds, 1997), to model *Avena barbata*, the dominant species of the Jasper Ridge ecosystem. We had no prior experience with GePSi, so this exercise addresses several of the concepts presented in this volume concerning the purported benefits of genericness, modularity, and object-oriented programming (OOP) in plant modeling. The objective of this paper is to briefly summarize the extent to which these benefits were realized and some of the problems encountered. In particular we seek to answer the following questions. In the case of GePSi, what does 'generic' actually mean in terms of applying the model to a new system? Does the modular structure of GePSi, which is a relatively complex model, facilitate its transfer? Does this structure help researchers (other than its developers) understand and utilize the model? We first provide a brief description of GePSi—focusing on features related to its transferability—and then present our experiences in applying GePSi to the Jasper Ridge ecosystem.

2. Description of GePSI

2.1. Overview

GePSi is a generic, fully modular, plant simulator implemented in the OOP language, C++. GePSi follows the design criteria and rules for modularity and genericness described by Reynolds and Acock (1997). The implementation of such models is greatly facilitated by the use of C++ since the object-oriented features of this language encourage modularity. There is a direct parallel between the computer program's representation of plant variables in the model and the natural, physical components of plants, e.g. stems, roots, flowers, and leaves (Sequeira et al., 1997).

The classes in GePSi are arranged in a kind-of hierarchy (see Fig. 2 in Chen and Reynolds, 1997). These hierarchies define the inheritance relationships between classes (akin to a family tree). In OOP, each class inherits the methods (i.e. operations) and attributes (i.e. data) from its superclass. Inheritance is an essential feature of OOP since it provides the ability to design a class with general features and then derive specific cases from it. We were hopeful that this feature would facilitate the transfer of GePSi from a woody plant to a grass model.

GePSi is composed of two major parts: abiotic and biotic. The reader is referred to Chen and Reynolds (1997) for details of the various processes considered in the model. The abiotic part of the model contains driving variables for the aboveground aerial environment and the below-ground soil environment. In the aboveground, the class weather defines the weather conditions above a canopy and MicroWeather defines the vertical profiles of micrometeorological variables in a canopy (Fig. 1). The belowground soil environment contains one class, SoilProperty, with three subclasses that define vertical profiles of physical and chemical variables in a soil column.

The biotic part of GePSi combines modules describing canopy photosynthesis and energy balances, the root environment, water relations, and potential growth dynamics to generate whole-plant carbon, water, and nitrogen balances. In general, GePSi is a mechanistic model, that considers such processes as photosynthesis, gas and energy fluxes in the canopy, and carbon and nitrogen partitioning between plant parts. Photosynthesis is described by a canopy module based on the leaf photosynthesis model of Farquhar and von Caemmerer (1982), as modified by Harley et al. (1992). Gas and energy fluxes in the canopy are described by the canopy microclimate model of Caldwell et al. (1986), as modified by Reynolds et al. (1992). Carbon and nitrogen partitioning follow the functional balance theory to maintain balanced growth between roots and shoots (Brouwer, 1962; Davidson, 1969).

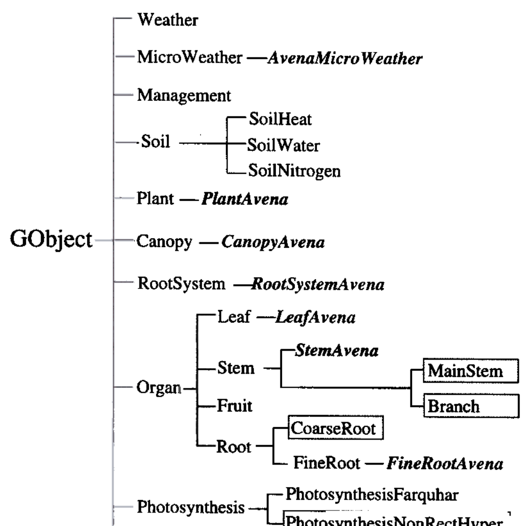

Fig. 1. The hierarchical class structure of the GePSi model used to model loblolly pine (i.e. Fig. 2 in Chen and Reynolds, 1997) showing modifications that were made to model *A. barbata*. Classes not used are enclosed in boxes and new classes are shown in italic boldface.

2.2. Genericness

Like most 'generic' plant models, which tend to be focused on a single species (e.g. Acock and Reddy, 1997; Lemmon and Chuk, 1997; Sequeira et al., 1997), GePSi was initially developed by Reynolds et al. (1980) to model two species: loblolly pine (*Pinus taeda*) and the desert shrub, creosotebush (*Larrea tridentata*). Hence, it was originally designed to deal only with woody shrubs and trees. The version of GePSi in use prior to this study emphasized the response of *P. taeda* to elevated [CO_2], which has been studied extensively by B.R. Strain and colleagues at Duke University for a number of years (e.g. Griffin et al., 1995; Larigauderie et al., 1994; Lewis et al., 1994; Thomas et al., 1994; Tissue et al., 1993). That version of GePSi included processes that are common to many plant species: photosynthesis, respiration, carbon partitioning, phenology, growth, nutrient dynamics, and water relationships. In principle, a model that incorporates these common processes can be used to predict the growth and development of other functionally equivalent species (hence, the use of the term 'generic' to describe GePSi).

Reynolds and Acock (1997) describe three practical ways to achieve genericness in models. In case no. 1 the structure of a model remains fixed and is simply re-parameterized with species- and site-specific parameters. Since GePSi was developed for woody trees and shrubs, it was not reasonable to expect that we could simulate a grass species simply by using different parameter values. In case no. 2, stand-alone process modules (e.g. photosynthesis, carbon allocation, nutrient uptake, etc.) are used as building blocks to develop a plant growth model once the appropriate interfaces between these modules are devised. This also does not describe GePSi since interfaces for the modules are fully defined and have been implemented. Thus, in the case of Jasper Ridge, we considered GePSi to be 'generic' in the sense of

Table 1
Correspondence between classes in GePSi, input data required to parameterize the classes, and experimental measurements made the Jasper Ridge CO_2 project

Class	Input data required	Experimental measurement
Microclimate	Radiation, precipitation, temperature, humidity, CO_2, wind	Weather data from a station near the experimental sit
Soil environment	Temperature, water, and nitrogen	Soil water contents measured by TDR (Fredeen et al. 1995); N mineralization (Hungate et al., 1996)
Canopy	Stratified canopy structure based on stem height, leaf area	Light interception by the canopy
Photosynthesis	Farquhar and von Caemmerer (1982) model	A/C_i curves of *Avena barbata* in field; *A. sativa* in laboratory (Jackson et al., 1995)
Respiration	Maintenance, growth respiration, as a function of temperature	No measurements
Partitioning	Partitioning coefficients	Root/shoot ratio, leaf/root ratio (G. Joel, unpublished)
Growth	Increment of biomass based on available photosynthate	Biomass data twice a year in field (Field et al., 1996)
Phenology	Phenology as a function of degree-days	Chiariello (1989); recorded flowering time as affected by $[CO_2]$

Reynolds and Acock's case no. 3, in which a set of modules—and the interfaces between them—are both fully defined. In theory, we expected that some of the modules could be reused without alteration, some would only require re-parameterization, and some would be completely rewritten, although they would retain the same interfaces. In practice, the question was: what would really be required to apply the generic model to other species?

3. Applying GePSi to Jasper Ridge

3.1. Structural modifications

With the help of its developers (Drs. J.-L. Chen and J.F. Reynolds), we initially compared the general structure of GePSi with the major biotic and abiotic field measurements being made in the Jasper Ridge CO_2 project. The minimum set of modules that were deemed necessary to model *A. barbata*, along with the corresponding experimental data needed to parameterize them, are shown in Table 1. The class hierarchy for the *Avena* version of the model, as modified from the *Pinus* version, is shown in Fig. 1.

Radiation, daily temperature (including minimum, maximum and mean temperature), precipitation, and wind speed are recorded in a weather station ca. 500 m from the experimental site. These data were used directly as inputs to weather. The classes management, SoilProperty (including subclasses SoilHeat, SoilWater, and SoilNitrogen), and TimeCourse provide representative variables and operations that *A. barbata* shares with *P. taeda*. Therefore, we did not change the structure of these classes (Fig. 1) but relied solely on re-parameterization (see below).

In GePSi, the class organ contains the shared characteristics of leaves, stems, fruits, and roots (i.e. each is a 'kind-of' organ). The leaf class is a subclass of organ, thus leaf inherits its characteristics. After extensive examination of the photosynthesis and organ classes, we determined that the functioning of *A. barbata* and *P. taeda* were similar enough that we could use these classes with no changes (Fig. 1). Again, this implies that the appropriate parameterization of these classes will adequately describe both pines and grasses. However, we did ask the developers to derive several new classes to specifically describe *Avena*.

To model loblolly pine, GePSi had two subclasses of stem: MainStem and BranchStem, that were used to study stem elongation and canopy

Table 2
Comparison of parameters for various carbon processes used in the Avena and Loblolly pine versions of GePSi

Process/parameter	Jasper Ridge (*Avena barbata*)	Loblolly pine (*Pinus taeda*)
Photosynthesis[a]		
V_{cmax} (μmol m^{-2} s^{-1})	45	18
J_{max} (μmol electrons m^{-2} s^{-1})	100	38.5
R_d (μmol m^{-2} s^{-1})	0.16	0.16
Respiration rates		
$R_{m, maintenance}$ (μmol m^{-2} s^{-1})	0.04	0.02
$R_{g, growth}$ (μmol m^{-2} s^{-1})	0.33	0.33
Partitioning between root and shoot (fraction)	0.35	0.28
Carbon storage (g d^{-1})	0.20	0.15
Root exudation rate (g d^{-1})	0.02	N/A
Leaf Senescence rate (g d^{-1})	0.025	0.001
Specific Leaf Area (m^{-2})	0.025	0.037
Root death rate (g d^{-1})	0.04	0.01

structure (Fig. 1). These subclasses were derived from WoodyStem, i.e. they inherited the variables and operations that define functions and properties unique to stems. WoodyStem separates hardwood, sapwood and active growing tissues and each has a different respiration rate. In addition, WoodyStem determines the heights where leaves grow, which ultimately affects canopy structure. Many of these features were not required for *Avena*. Therefore, using the inheritance feature, the developers created a new class StemAvena from the class stem. In StemAvena, they eliminated hard and sap wood tissues but kept growing tissue.

Due to the small stature of the plants and short growing seasons, the canopy structure of the *Avena*-dominated grasslands at Jasper Ridge is not well-developed compared to *P. taeda*. Leaf area index is usually < 1 in the serpentine grassland and about 2 in the sandstone grassland during the peak growth period. Thus, as a first approximation, we treated the grassland canopy as a 'big leaf'. To do this, the class Canopy was modified to create the class AvenaCanopy. To correspond with the 'big leaf' representation of the canopy, the developers greatly simplified MicroWeather to drive the biological processes (Fig. 1) since detailed canopy microclimate was not warranted. This eliminated a significant amount of detail.

3.2. Re-parameterization

GePSi requires a large number of parameters (ca. 200), ranging from photosynthetic enzyme activities to soil hydraulic conductivity. As expected, some aspects of the re-parameterization were straightforward whereas other aspects were less so. GePSi has a large database to provide parameter values for different types of soils, which allowed us to quickly re-parameterize the SoilProperty class for Jasper Ridge. The photosynthesis class was parameterized using both field and laboratory measurements of A/C_i (assimilation/intercellular [CO_2] and A/I (assimilation/irradiance) curves for the species *Avena sativa* and *A. barbata* (Jackson et al., 1995). Parameters associated with carbon processes in the model are shown in Table 2 .

Estimating parameter values for the remaining processes required several steps. First, we focused on those parameters associated with plant carbon dynamics, including carbon release through plant respiration, carbon partitioning into various organs, root carbon exudation, and turnover of soil carbon. After estimating parameter values for the model—based on available field data, literature values, and (in some cases) guesses—we ran the model and compared predictions to experimental results. We repeated these processes until we obtained an acceptable fit to the experimental data. This inevitably led to some re-parameterization of other processes, including nitrogen dynamics and water relationships.

3.3. Application of model

The structural modifications and re-parameterization described above required approximately two weeks. Once we were satisfied with the behavior of the *Avena* version of GePSi, we used it to examine the response of the Jasper Ridge grasslands to elevated [CO_2]. Specifically, we examined the paradox that under elevated [CO_2] concentrations, there is often an increased photosynthetic carbon uptake in plants but this does not necessarily result in a proportional increase in plant biomass. We evaluated the effects of various possible physiological adjustments on plant growth and carbon balance of the dominant species, *A. barbata*, using GePSi. In the absence of physiological adjustments, an observed 70% increase in leaf photosynthesis at 70 Pa [CO_2] was predicted to increase plant biomass by 97%, which was inconsistent with observed changes of −5, −13, and +40% in biomass in 1992, 1993, and 1994, respectively. Simulations were conducted in which we explored the consequences of changes in various physiological parameters: carbon allocation to roots, leaf death rate, nonstructural carbohydrate storage, leaf mass/unit area, and various combinations of these. This modeling exercise suggested that although these adjustments differentially affect root versus shoot growth and seasonal carbon fixation, all lead to reduced carbon use efficiency and leaf area development. Details of this study are provided in Luo et al. (1997).

4. Discussion

The contributors to this special issue on the use of modularity in plant growth models unanimously deem the modular, generic approach useful for reducing duplication of effort in model development and for facilitating the interactions of developers and users. Some of their expectations were tested in this study. The 'developers' of the generic plant simulator (GePSi) were Chen and Reynolds (1997); the 'users' were the authors of this paper—who had no prior experience with the model. We adapted GePSi to simulate the dominant species of the Jasper Ridge ecosystem. While this is only a single case study with a single model, we think that our experiences are likely to be of general interest. Our evaluation is presented in terms of: (1) design considerations, including the importance of how the modules and classes in GePSi were defined; and (2) the implementation phase, which critiques the use of OOP for facilitating the transfer of the model.

Since GePSi was designed following the modular design criteria outlined by Reynolds and Acock (1997), it is purported to be more understandable to potential users than previous efforts in generic model-building (e.g. Reynolds et al., 1980). The understandability design criterion states that modules (e.g. the classes shown in Fig. 1) should be understandable as stand-alone entities, without the need to refer to other modules in order to grasp what they do. In this regard, GePSi was an outstanding success. With the developers providing a guided tour of the model, we were able to quickly select those individual modules that were relevant to specific research hypotheses of the Jasper Ridge CO_2 project, e.g. the paradox of increased photosynthetic carbon uptake that is not accompanied by a proportional increase in plant biomass (see above). Within 2–3 days, we had a good comprehension of GePSi—both its strengths and weaknesses—as a model for addressing the effects of elevated [CO_2] on plant and ecosystem processes at Jasper Ridge.

The understandability criterion is closely related to the decomposability criterion, which states that a good modular design divides the main problem into small, independent subproblems (modules), each of which can be worked on separately (Reynolds and Acock, 1997). In this study the developers were able to quickly and efficiently improve various components of the model that the users considered inadequate (e.g. root growth, root exudation, carbon allocation, etc.). These changes were made as independent activities. The changed modules were then incorporated with ease by the developers into the final *Avena* model as they were completed.

In terms of implementation, the results were mixed. We encountered the following paradox: implementing GePSi in C++ resulted in a better designed product—it was relatively easy to understand what the model did and how—but this also meant that it was not easy for us to work independently with the model since we were not familiar with C++. The cost of working in C++ without prior experience is extremely high (see discussion in Lemmon and Chuk, 1997) and GePSi was not designed with good user interfaces. Thus, the adaptation of GePSi to the Jasper Ridge site had to be done in close cooperation with the developers. On the plus side, the object-oriented paradigm afforded the developers excellent flexibility to modify GePSi to simulate grasses. As described above, the structural changes were relatively straightforward due to the hierarchical class structure and inheritance features of C++. Consequently, in order for the model to be accessible to users, independent of the developers, it will be necessary to develop the appropriate user interfaces for the steps described above (Section 3). This will require a major effort but we see no alternative.

Is GePSi generic? Yes, in the sense of Reynolds and Acock (1997) case no. 3, whereby a set of modules and their interfaces were fully defined and some of the modules were used without alteration, some only required a re-parameterization, and some were completely rewritten, although the same interfaces were retained. Of course, the emphasis in developing GePSi has been on plant and ecosystem response to elevated [CO_2], which was also the intended use of the model for the Jasper Ridge study. If, on the other hand, we had wanted to simulate plant competition or successional dynamics, or to examine the role of ABA on root and stomatal activities, the use of GePSi would probably not have been as straightforward. The essentials of the basic model might still have been useful for such applications but major modifications would have been needed to provide the appropriate emphasis. This type of extension of GePSi remains to be tested.

In summary, we believe that the most immediate and significant impact of the use of generic, modular models, such as the generic plant simulator (GePSi) described in this paper, will be in facilitating the interactions of developers and users and reducing duplication of effort in model development.

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Abstract

In order to conduct modeling studies on the effects of elevated atmospheric carbon dioxide concentration ([CO_2]) on plant and ecosystem processes at the Jasper Ridge grassland in northern California, the generic plant simulator (GePSi) (Chen, J.-L. and Reynolds, J.F., 1997. Ecol. Model., 94: 53–66), is modified to simulate grass dynamics. This modification was attempted by the authors of this paper, who had no prior experience with the model. Prior to this project, GePSi, which is implemented in the object-oriented programming (OOP) language, C++, had only been used to model trees and woody shrubs. This exercise addressed several of the concepts presented in this volume concerning the purported benefits of genericness, modularity, and OOP in plant modeling. The objective of this paper is to briefly summarize the extent to which these benefits were realized and some of the problems encountered. Our evaluation is presented in terms of: (1) design considerations, including the importance of how the modules in GePSi were defined; and (2) the implementation phase, which critiques the use of OOP for facilitating the transfer of the model. This study suggests that generic, modular models such as GePSi will facilitate the interactions of model developers and users and reduce duplication of effort in model development. © 1997 Elsevier Science B.V. All rights reserved

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