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Optimizing simulated fertilizer additions using a genetic algorithm with a nutrient uptake model

Wendell P. Cropper Jr.*, N.B. Comerford

School of Forest Resources and Conservation and Department of Soil and Water Science, Institute of Food and Agricultural Science, University of Florida, P.O. Box 110410, Gainesville, FL 32611-0410, USA

Abstract

Intensive management of pine plantations in the southeastern coastal plain typically involves weed and pest control, and the addition of fertilizer to meet the high nutrient demand of rapidly growing pines. In this study we coupled a mechanistic nutrient uptake model (SSAND, soil supply and nutrient demand) with a genetic algorithm (GA) in order to estimate the minimum addition of phosphorus necessary to meet the initial four-year demand. Optimal P additions were estimated using two pine root length density inputs scenarios, a mycorrhizal scenario, and a grass competition scenario. The low root length scenario required $32.5–35.0 \, kg \, P \, ha^{-1}$ (depending on the fitness criteria) to best match the four-year loblolly pine P demand. With higher root length density, only $14.5 \, kg \, P \, ha^{-1}$ was required to meet demand. Adding a large fungal length density of mycorrhizae changed the simulated P uptake kinetics so that two separate fertilization amendments were optimal, although the total P added was similar to the higher root scenario. GA fitness functions were adjusted to eliminate SSAND uptake underestimates smaller than loblolly P demand, at the cost of an additional $9 \, kg \, ha^{-1}$ (higher root scenario) or $1–2 \, kg \, ha^{-1}$ (mycorrhizal scenario). Optimal GA estimates for P addition with grass competition were $1.5–3 \, kg \, ha^{-1}$ higher, with a sharp fitness peak associated with decline of grass in the first growing season.
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1. Introduction

The importance of intensive management of pine plantations in the southeastern United States is rapidly increasing. This management regime typically includes suppression of competitors and pests, deployment of genetically improved trees, and additions of nutrients to promote fast growth. This type of management regime can result in a two or three fold increase in growth (Allen et al., 1990; Colbert et al., 1990; Jokela and Martin, 2000). As a strategy to help reduce the impact of this management system and to decrease costs, it is useful to minimize nutrient additions while meeting the demand imposed by rapid growth.

* Corresponding author. Tel.: +1 352 846 0859; fax: +1 392 1707.
  E-mail address: wcropper@ufl.edu (W.P. Cropper Jr.).

In order to understand and manage the nutrition of rapidly growing tree species, it is necessary to understand the ability of soils and root systems to meet the demand. Computer simulation models have been applied to this optimization problem at scales ranging from Barber–Cushman mechanistic simulations of tree nutrient uptake (Kelly and Ericsson, 2003) to empirical crop models linked to GIS systems for large-scale simulations (Tianhong et al., 2003).

As a test case for addressing this problem, we applied the nutrient uptake subroutine of the SSAND (soil supply and nutrient demand) mechanistic model, simulating four years of nutrient uptake characteristic of intensive loblolly pine (*Pinus taeda*) plantation development in the southeastern coastal plain. The nutrient uptake component of SSAND is a revision and upgrade of the COMP8 model described by Smethurst and Comerford (1993).

Although operational fertilizer additions at the study site included a range of macro and microelements; in this study we only address phosphorus (P) additions. Sandy coastal plain soils are typically low in weatherable minerals, with significant fertilizer growth responses to N and P fertilization commonly observed (Pritchett and Llewellyn, 1966; Gholz et al., 1985).

Determination of an optimal fertilizer regime is potentially a high dimension problem. Variables for multiple fertilizer additions could include the time(s) of application and the amounts and forms of one or more nutrients. Genetic algorithms (GA) are likely to be useful approaches for optimizing multivariable problems (Wilson, 2000). Genetic algorithms are a type of evolutionary computer program that mimics the process of natural selection (Mitchell and Taylor, 1999). Using GAs, it is feasible to test a large number of possible solutions in parallel, to select the best solutions based on fitness criteria, and to introduce novelty through stochastic mutation and combination of traits that are analogous to sexual reproduction. Applications of the GA techniques include model parameter estimation (Cropper and Anderson, 2004), drug and electronic circuit design, image processing, and optimization (Cropp and Gabric, 2002; Koza et al., 2003).

It is possible to use the nutrient uptake routine of the SSAND model to repeatedly simulate P fertilization experiments with variable fertilizer amounts and timing of additions. However, this could be a time consuming exercise with no assurance that the final fertilization prescription was optimal. In this study, we have linked the SSAND model with a genetic algorithm code in order to provide a rapid objective method of estimating the minimum P addition necessary to meet the four-year demand, and to develop a general template for more complex fertilizer optimization problems.

2. Site description

The data used for these simulations came from a study of 10 stands of fast-growing loblolly pine plantations 1–4 years of age in the coastal plain region of southern Georgia (Adegbidi et al., 2002, 2004) and a study of one-year-old slash pine (*Pinus elliottii* var. *elliottii*) on similar soils in northern Florida (Smethurst et al., 1993a,b; Smethurst, 1992). Detailed methods for root distributions, biomass estimation and stand nutrient contents that yielded estimates of nutrient uptake are from Adegbidi et al. (2002, 2004) and unpublished data. Briefly, all 10-sample plantations of loblolly pine were genetically improved one-year-old l seedlings planted at a 1.8×3.7 m spacing growing on Spodosols that contained an argillic horizon in the subsoil (sandy, siliceous, thermic ultic alaquods and oxyaquic alorthods). Herbicides were used to control understory plants the first two growing seasons (e.g., hexazinone, sulfometuron, imazypyr, glyphosate). All sites were fertilized with nitrogen (N) and phosphorus (P) applied at elemental rates of 30 and 33 kg ha^{-1}, respectively in the first growing season, and were refertilized in the third growing season with N, P, K and B applied at rates approximating 90, 25, 40 and 1.5 kg ha^{-1} of the elements, respectively.

Three replicate stands, spatially distinct, were sampled within each age class for root distribution (Adegbidi et al., 2004), biomass (Adegbidi et al., 2002) and nutrient content. Sampling was carried out in the early fall of 1999 and 2000. The one slash pine site was planted with genetically improved slash pine seedlings and weeds were either totally controlled in the first year or left alone. Mean annual precipitation for all sites ranged from 1250 to 1300 mm, while mean annual temperature averaged about 19.5 °C.

Adsorption and desorption isotherms for phosphorus were based on Smethurst (1992). Initial solution concentrations prior to fertilization were taken from Smethurst et al. (1993a). Soil water content is based on

water content values during a typical year as measured by Phillips et al. (1989). The constant phosphorus mineralization rate was based on the work of Polglase et al. (1992) and Grierson et al. (1999). The equation for impedance was taken from Bruggeman (1935). Water flux rate was based on total fine root density (Adegbidi et al., 2004) and average estimates of transpiration. Finally, the Michaelis–Menten parameters for P uptake of loblolly pine were the values used by Smethurst et al. (1993b) for slash pine.

3. SSAND model

The SSAND model (soil supply and nutrient demand) is a nutrient management model developed as a subroutine for a plant growth model. This study used the nutrient uptake and fertilization routines in SSAND. This routine is a revised version of the COMP8 model described in detail by Smethurst and Comerford (1993) and used with pine and bahiagrass by Smethurst et al. (1993), Comerford et al. (1994) and Ibriki et al. (1994). As described in Smethurst and Comerford (1993), COMP8 was based on calculating mass flow and diffusion of a nutrient through the soil based on soil physical and chemical parameters in order to simulate the nutrient concentration at the root's surface. Nutrient uptake was controlled by the amount of root surface area and the concentration at that surface via a Michaelis–Menten kinetic equation. Nutrient movement from the solid phase to soil solution is through either mineralization or desorption as described by a Langmuir or Freundlich isotherm.

The major revisions made to COMP8 as it was incorporated into SSAND were (1) rewriting the code from procedural Basic to an object oriented implementation in Visual Basic 6.0 or Python (used in this study), (2) making it more interactive via input data forms, (3) the addition of mycorrhizal hyphae, (4) a fertilization routine that used the partition coefficient of nutrient sorption onto the mineral soil to distribute fertilizer between solid and liquid phases and then used desorption partition coefficients to release the nutrient to the soil solution as the nutrient was removed from solution and (5) allowing mineralization rate, water content, root length density and extramatrical mycorrhizal hyphal length density to change with time steps via user de-

fined input files. Like COMP8, SSAND is based on the discussions of Nye and Tinker (1997) and is similar in theory to models described Barber and Cushman (1981) and similar in theory and approach to that used by Yanai (1994) and Williams and Yanai (1996).

The model can be run from an input file or input data sheets. In our case we used a prepared input file that included soil horizon volume, initial soil solution concentration, soil water content, bulk density, diffusion coefficient of $H_2PO_4^-$ in water, P mineralization rate, parameters of the soil impedance equation, parameters for P sorption and desorption Freudlich equations, water influx rate to the root, Michaelis–Menten parameters, root radius, and a root growth file. The model works on a time step basis using solution concentration and water influx to the root to control mass flow and the desorption/sorption isotherms, water content, impedance and bulk density to control soil solution concentration and the rate of nutrient flux to roots by diffusion. Mineralized P or P added via fertilization reacts with the soil surface via the Freundlich sorption isotherm to control the solution concentration. A depletion zone propagates with time from the surface of the root or hypha to the no-transfer boundary. When the depletion zone reaches the boundary, the root is using the entire soil volume assigned to it as a resource and inter-root competition initiates. The user can define fertilizer additions (number of events, timing of events and amount of fertilizer per event) for selected nutrients. Comparing the uptake over time with a desired, user-defined uptake curve helps evaluate how well the fertilizer regime meets the crop need.

4. Simulation scenarios

Mechanistic nutrient uptake models are sensitive to root length density (Smethurst and Comerford, 1993; Yanai, 1994; Williams and Yanai, 1996). In this study we assumed two scenarios of pine root length density (*ROOT1* and *ROOT2*) and used the *ROOT2* data coupled in two additional scenarios with mycorrhizae and with a competing grass species (Fig. 1). The mean *ROOT2* root length density ($0.172 \, \text{cm cm}^{-3}$) was more than twice that of the *ROOT1* input data ($0.076 \, \text{cm cm}^{-3}$) over the entire study period. Linear interpolation between input value dates provided daily

Pine Root Length Density
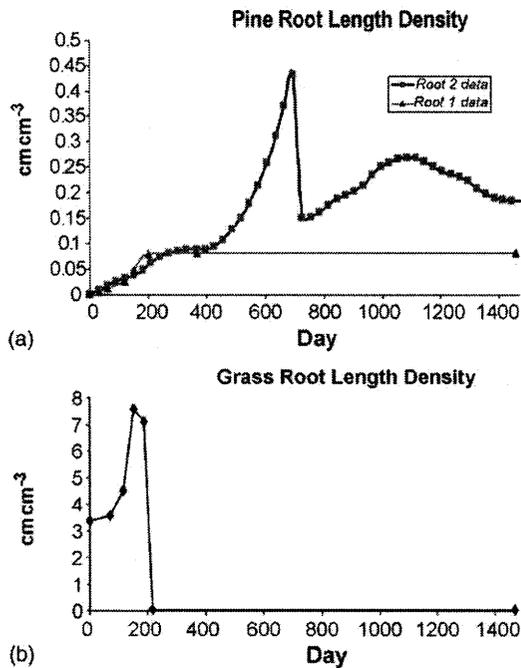

(a)

Grass Root Length Density

(b)

Fig. 1. Root length density inputs for simulation scenarios: (a) *ROOT1* and *ROOT2* scenarios, (b) grass competition scenario.

estimates of root length density. The grass competition scenario used measured grass root length density through day 187, followed by a linear reduction to $0.05\,\mathrm{cm\,cm^{-3}}$ at day 217 through the end of the simulation. Symbiotic mycorrhizae are ubiquitous, often playing a significant role in plant P uptake (Tinker and Nye, 2000). Due to the difficulty in estimating mycorrhizal length density in the field, we assumed that mycorrhizae had a radius of 0.002 cm and a variable length density of 80 times the *ROOT2* (time) input data.

5. Genetic algorithm

We based the Python implementation of the GA used in this study on the scheme described in Wilson

(2000) to estimate optimal reproductive allocation in plants subject to simulated herbivory. The GA (Fig. 2) was initialized with a population of 250 or 500 sets of fertilization parameters for the SSAND model. Each of these sets (individuals) consisted of uniform random selections of one or two P addition amounts (0–45 kg/ha) and dates of fertilization (5–1460). It is likely that better fits of uptake and demand could be achieved by increasing the number of allowed fertilization events beyond two, but it is also likely that operational costs would be prohibitive with such prescriptions.

In each generation (Fig. 2) we ran the SSAND model for each individual set of parameters, followed by a calculation of fitness for each individual. We ran the GA for 25 generations, with outputs of the parameters of the individual with the highest fitness for each generation. A variety of fitness functions were used to assess the match between simulated P uptake and pine P demand. An optimal solution depended on minimizing the value of the fitness function. The first fitness function was:

$$\text{Fitness} = \sum_{\text{day}=1}^{1460} (\text{uptake}_{\text{day}} - \text{demand}_{\text{day}})^2 \qquad (1)$$

where uptake was the cumulative P uptake for each day of the simulation ($\mathrm{kg\,ha^{-1}}$), and demand was the product of loblolly pine biomass (kg) and P concentration ($\mathrm{kg\,P\,kg\,biomass^{-1}}$). We based other fitness functions on:

$$\text{Fitness}_{\text{day}} = \begin{vmatrix} \dfrac{\text{uptake}_{\text{day}}}{\text{demand}_{\text{day}}} & \text{when uptake}_{\text{day}} \geq \text{demand}_{\text{day}} \\ 1 - \left(\dfrac{\text{uptake}_{\text{day}}}{\text{demand}_{\text{day}}}\right) & \text{when uptake}_{\text{day}} < \text{demand}_{\text{day}} \end{vmatrix} \qquad (2)$$

summing over one, two, four, or 12 selected comparison dates. For this fitness function, the goal was to minimize the difference between calculated $\text{Fitness}_{\text{day}}$ and 1. We added additional fitness criteria to some runs using Eq. (2) based on conditions when the uptake was less than demand at a comparison date (an underestimate). One form of this additional rule was that $\text{Fitness}_{\text{day}}$ was set to zero for an underestimate, and the other form defined the summed fitness of the individual as zero for any comparison date with an underestimate, ensuring no representation for that individual
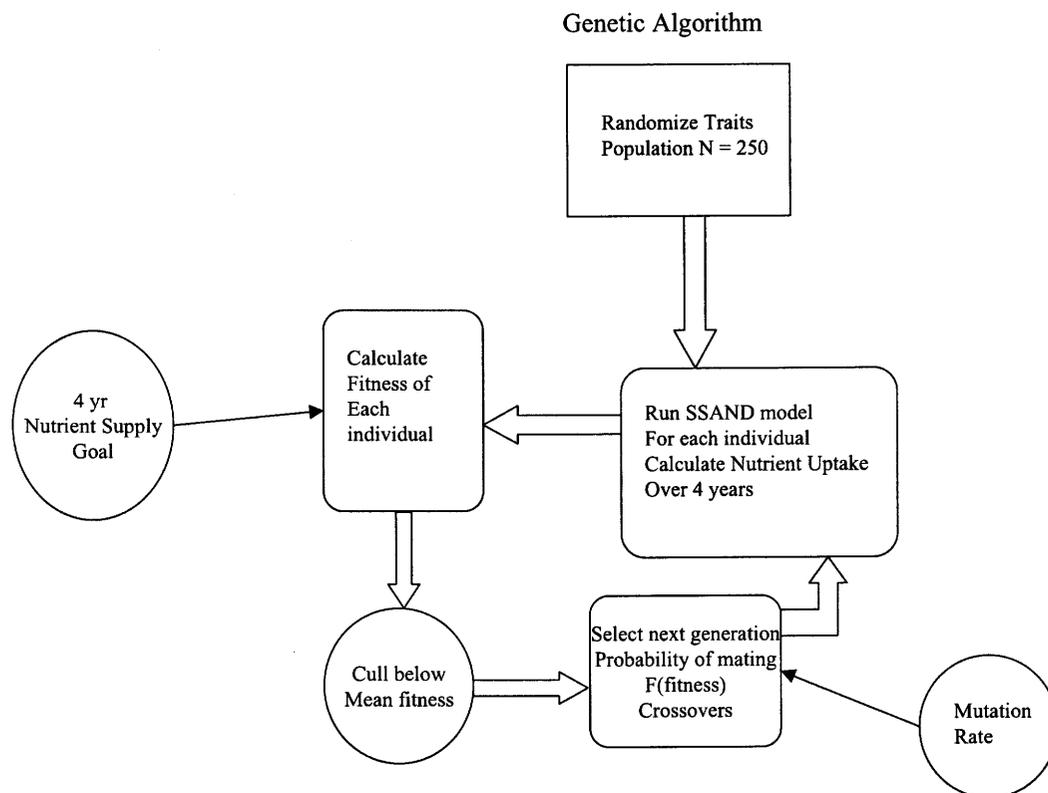
Genetic Algorithm

Fig. 2. Flowchart for the genetic algorithm used to optimize SSAND phosphorus additions.

in the next generation. Representation in subsequent generations depended on processes analogous to sexual reproduction, mutation, and natural selection in biological populations. We eliminated all individuals in the population with fitness below the population average prior to reproduction. New individuals were generated from two parents with equal probability of selection of parental traits (P addition amount, and independently date of addition). The probability of reproduction was directly proportional to individual fitness. We assigned a per trait mutation rate of 0.01. An individual mutation was implemented as a random selection of a trait value within the entire allowable range. Mutations are designed to reduce the chance that the solution becomes trapped in a local optimum. The appropriate mutation rate and population size for a GA are difficult to specify a priori. A small population usually becomes rapidly fixed at a poor solution, and a high mutation rate will prevent combinations of fitter characteristics from per-

sisting. A mutation rate that is too low may increase the probability of missing the parameter space near the global optimum. In order to test the importance of mutation rate, we repeated a two-date fertilization scenario with the GA mutation rate increased from 0.01 to 0.05.

6. Results and discussion

The initial scenario we tested was using the *ROOT1* root length density input (Fig. 1) with no mycorrhizae or grass competition. Using a fitness function of minimizing the sum of $(demand - uptake)^2$, the optimal fit was with 32.5 kg P ha^{-1} on day 239 (Fig. 3). The value of the fitness function for this scenario was 1902. Due to the seasonal variation in pine growth and to the relatively flat kinetics of simulated P uptake in this scenario, significantly better fits are not possible. The
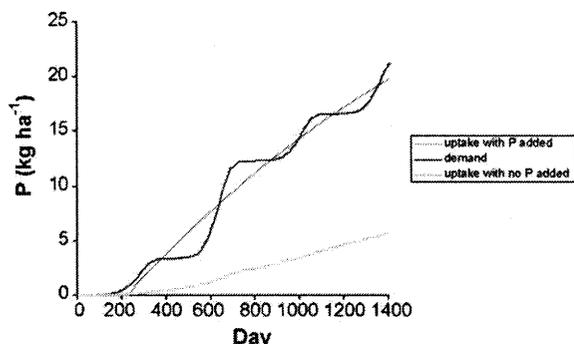
Fig. 3. Cumulative loblolly pine P demand, SSAND model simulated P uptake with 32.5 kg ha^{-1} added on day 239, and SSAND simulated uptake with no P added.

stochastic nature of the GA, as well as potential limitations imposed by the GA population size, parameter ranges, and number of generations, imply that GA optima estimates often differ from the true global optimum.

In order to investigate the fitness surface around the optimal value of 32.5 kg P ha^{-1}, we calculated fitness for a range of fertilization dates at the optimal addition level, and 3.5 kg P ha^{-1} above and below the optimal value (Fig. 4). The fitness surface around the GA optimum is complex, with different optimal fertilization dates associated with different amounts added. It is likely that a broad near-optimum region in parameter space exists between 32.5 and 36 kg P ha^{-1} added at days 200–300. More precision could be achieved, if desired, with another GA optimization focused on the near-optimum region (see grass competition scenarios below).
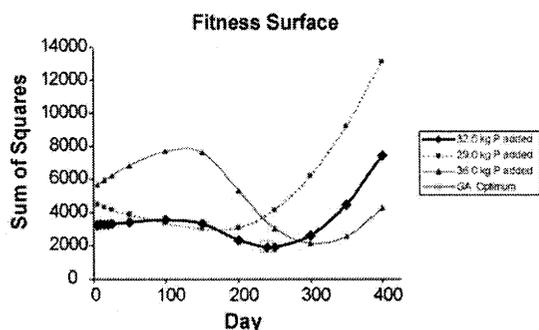

Fig. 4. Fitness values (daily sum of (demand − uptake)^2) for the GA optimum (32.5 kg P ha^{-1} added) and two other levels of addition.

Although the fitness function based on minimizing the sum of squares is a standard in optimization problems, GA s can be constructed using a flexible array of alternatives. With a fitness function based on minimizing the difference between the cumulative day 1460 demand and SSAND simulated uptake, we found many near perfect solutions (35 kg P ha^{-1}, added on days 67–242). Although these solutions meet the criterion of the fitness function, they are not typically good solutions for minimizing the sum of squares for the entire 1460-day growth period. Increasing the number of comparison dates to only two (GA optimum of 35 kg P ha^{-1} added at day 248) led to a solution with a fitness of 2672. This solution is within the broad near-optimal parameter space region (Fig. 4).

Using higher root length density inputs (the *ROOT2* data scenario) dramatically changed the GA optimum. In this case, a P addition of 14.5 kg ha^{-1} on day eight produced a fitness value of 1934. With a four comparison date fitness function (four local maxima on the demand curve), the optimal P addition was 14.5 kg P ha^{-1} on day 64 (fitness = 1994). The high soil buffer capacity for P, coupled with diffusion limited root uptake (Tinker and Nye, 2000), makes root length density a critical variable. This soil could supply the same simulated cumulative P uptake with the *ROOT1* input, but it would take longer than four years to reach the *ROOT2* scenario level. The soil P resource is more efficiently exploited at higher root length densities, with a nearly linear response to root length in simulated four year P uptake.

Any underestimate (simulated P uptake < demand) over the four-year period potentially represents an inadequate fertilizer addition. Small underestimates of P uptake are probably not important due to measurement errors in biomass and tissue concentrations, as well as "luxury" uptake. In order to provide a conservative estimate of minimum P addition, we tested fitness functions designed to prevent underestimates.

Using a fitness function with four comparison dates and zero fitness assigned for any date with an underestimate, the optimal P addition was 23.4 kg ha^{-1} added on day 13 (sum of squares = 47,136). This solution still produced a small underestimate. Modifying the fitness function to a zero fitness for any comparison date underestimate resulted in an optimal P addition of 25.3 kg ha^{-1} on day five (Fig. 5A).

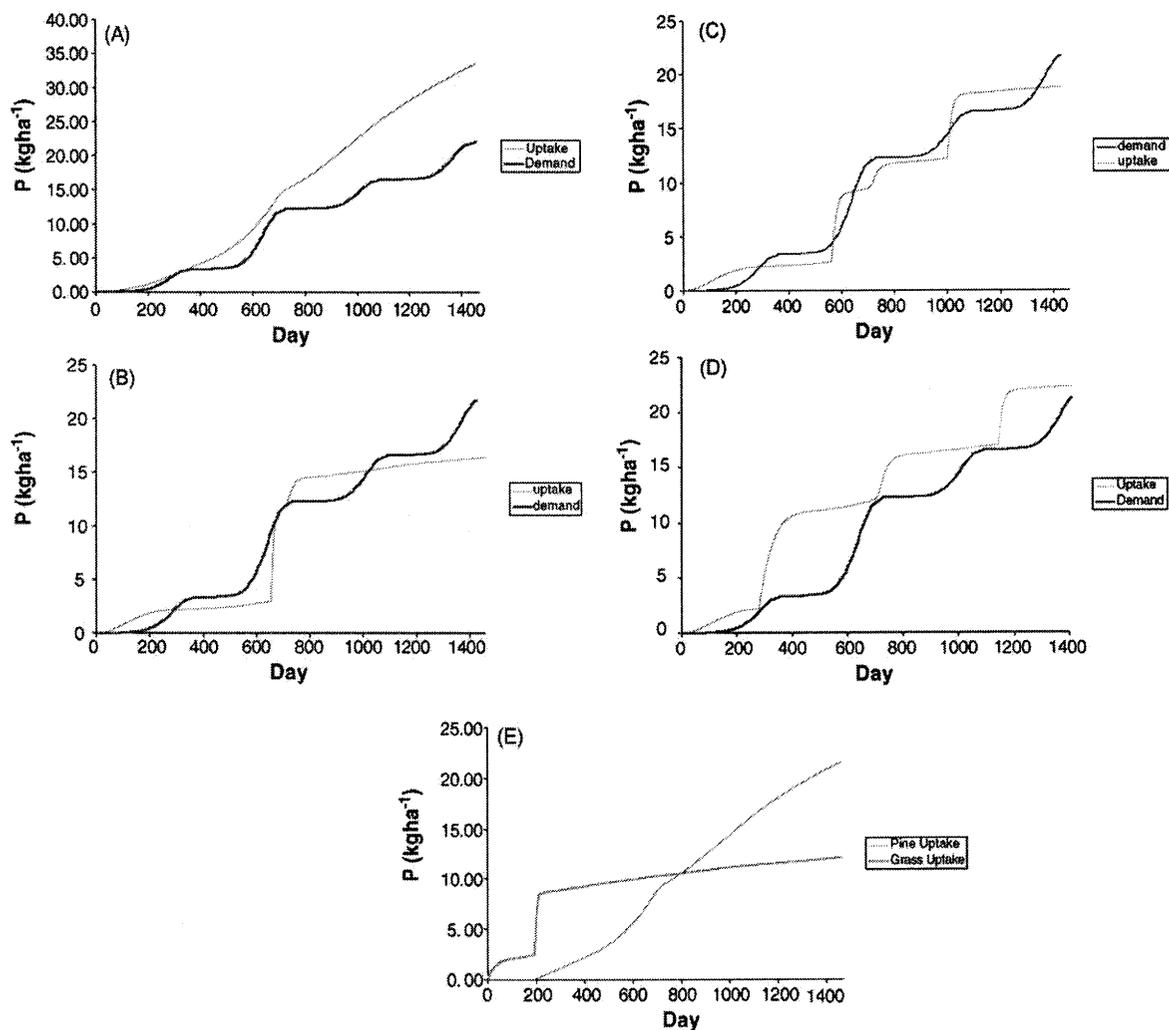Fig. 5. SSAND model simulated loblolly pine P uptake and demand: (A) with the GA optimum (25.3 kg P ha^{-1} added on day 5) and GA fitness function designed to eliminate underestimates; (B) optimal simulated loblolly pine P uptake and demand with mycorrhizae; (C) optimal simulated loblolly pine and mycorrhizal P uptake from two fertilization events; (D) optimal simulated pine and mycorrhizal P uptake with a GA fitness function preventing underestimates (uptake < demand); (E) simulation of grass and pine P uptake with a fertilization of 16.1 kg ha^{-1} on day 196.

7. Mycorrhizae scenarios

With a fitness function based on minimizing (uptake − demand)^2, a P addition of 9.85 kg ha^{-1} at day 654 was optimal (Fitness = 6147). The large increase in total absorbing surface associated with this scenario resulted in very rapid uptake of added P (Fig. 5B) and a poor fit relative to the root only scenarios.

We found a better GA fit of simulated P uptake to loblolly pine P demand when two fertilization dates were included (Fig. 5C). Optimal P additions were 7.3 kg ha^{-1} on day 564 and 6.6 kg ha^{-1} on day 1003 (Fitness = 2857). The optimal total P addition of 13.9 kg ha^{-1} with mycorrhizae was similar to the best single date addition amount (14.5 kg ha^{-1}) using the same fitness function. The inclusion of mycorrhizae in these scenarios influences the simulated kinetics of P

uptake much more than it changes the required total P supplement amount.

We repeated the GA optimization for this scenario with the mutation rate increased from 0.01 to 0.05. This run resulted in an optimal solution of 8.4 kg ha^{-1} added on day 609 followed by 4.1 kg ha^{-1} on day 1010. The difference between this run and the 0.01 mutation rate run is similar to the magnitude to the difference observed with repeat runs at the same mutation rate. The solution for mutation rate 0.05 had a Fitness value of 2608, or about 10% better than the 0.01 mutation rate optimum.

In order to provide a conservative estimate of the minimum P addition to meet demand, we altered the GA fitness function to match 12 comparison dates around four local maxima, and to set the fitness of any GA individual to zero following any underestimate of P demand. The GA optimum for this scenario (Fig. 5D) was 9.8 kg P ha^{-1} added on day 282 followed by 5.2 kg P ha^{-1} added on day 1146. Surprisingly, the total P addition for the more conservative scenario was only 0.5 kg ha^{-1} higher than for the two-date optimum minimizing (uptake − demand)^2. This optimal solution produced simulated uptake nearly equal to demand at several dates, but it would be easy to adjust the fitness function to add an additional buffer.

In addition to the rapid P uptake kinetics following fertilization, the pattern of simulated P uptake is strongly influenced by the root length dynamics. The *ROOT2* root length density inputs vary by a factor of four between day 400 and the end of the simulation. This effect is magnified by the addition of mycorrhizae as a constant 80× multiple of the pine root length density.

The response of the plant-mycorrhizal symbiosis to increased P availability is likely to be of critical importance. The fraction of arbuscular mycorrhizal infected roots is often depressed by high phosphorous supply in controlled conditions (Tinker and Nye, 2000), and might also be an important factor for ectomycorrhizal pine systems (Browning and Whitney, 1992). A scenario with a decreasing mycorrhizal length density as a function of P supply would produce results intermediate between the *ROOT2* scenarios with no mycorrhizae, and the 80× mycorrhizal scenarios reported here.

8. Grass competition scenarios

High intensity pine plantation management in the southeast coastal plain often includes suppression of herbaceous competitors. Grass species are significant components of pine plantation sites during the first few years of establishment (Ball et al., 1981; Conde et al., 1983). Understory suppression can lead to pine growth responses that are similar to the magnitude of fertilizer responses. Colbert et al. (1990) observed a 700%
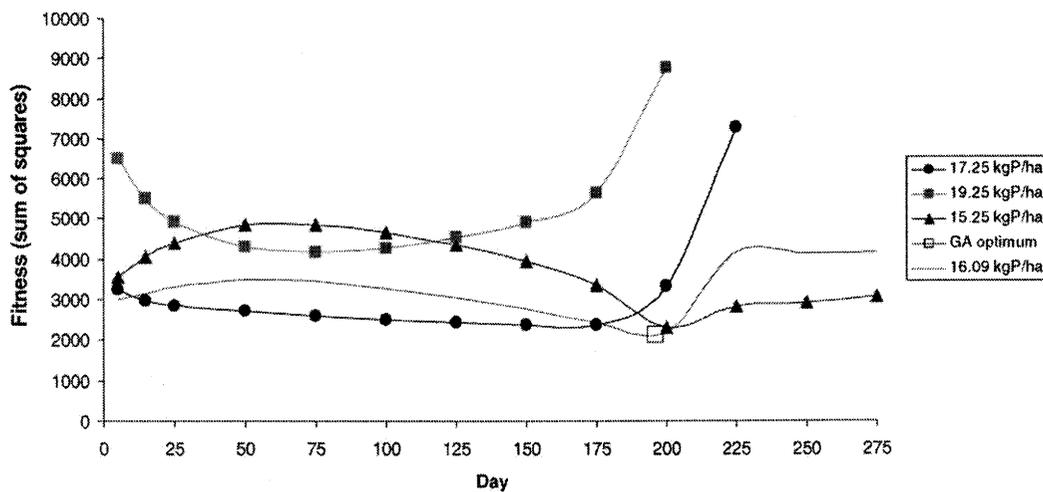

Fig. 6. Fitness values (daily sum of (demand − uptake)^2) for the GA optimum (16.1 kg P ha^{-1} added) and three other levels of addition.

increase in loblolly pine above ground biomass as a response to complete weed control. Using the SSAND model, the combination of grass at high root length density (Fig. 1) and *ROOT2* scenario pine roots, with a fertilization of 16.1 kg P ha^{-1}, leads to 12.1 kg P ha^{-1} grass uptake and 21.6 kg P ha^{-1} pine uptake (Fig. 5E). Seventy-one percent of the four-year cumulative grass P uptake is achieved by day 225.

With the grass scenario using the minimal sum of squares fitness function, the optimal P addition was 17.3 kg ha^{-1} at day 171 (Fitness = 2371). This P addition was less than 3 kg ha^{-1} more than the optimal solution without the grass competitor. The SSAND model is clearly predicting, as it does with the mycorrhizal scenarios, that the site is capable of supplying large P uptakes, if the root length density is adequate.

Examination of the fitness surface around the GA optimum led us to believe that the global solution was missed. The rapid drop of grass root length density near day 200 has an important influence on the optimal date of P addition. In order to improve the estimate of the optimal P addition, we ran another GA optimization with parameter ranges restricted to near the region of interest (13.25–19.25 kg P ha^{-1} during the first growing season). The optimal solution for this run (Fig. 6) was 16.1 kg P ha^{-1} added at day 196 (Fitness = 2150). The additional GA run only decreased the optimal P addition by 7%, but clearly demonstrated the possibility of "polishing" near-optimal solutions with additional iterations.

9. Conclusions

Optimal simulated P additions estimates from the GA procedure ranged from 10 to 35 kg P ha^{-1}, for the entire range of root length density, mycorrhizal, and competition scenarios. Even the more conservative scenarios designed to produce simulated P uptake consistently above the estimated loblolly pine demand only required additions of 16–25 kg ha^{-1}. These fertilization levels are considerably below the operational addition of 58 kg ha^{-1}. The actual fertilizer was applied in the form of di-ammonium phosphate (DAP). Fertilization with DAP was designed to meet both the N and P demand, and could potentially be well above the minimum requirement of one of the elements. With a multielement optimization, the constraint of element ratios based on DAP application could be easily accommodated.

We have found the GA optimization approach to be an effective and flexible method for estimating the minimum P additions necessary to meet the demand of rapidly growing loblolly pine trees. As with any simulation model, the results depend on the assumptions and particular inputs that were applied. Some of the parameters needed for the SSAND model (e.g. uptake kinetics for each species and mycorrhizal RLD) are poorly known, and may be quite important. Additionally, it is likely that the model could be improved with a dynamic linkage to mechanistic tree and hydrology models. Even small changes in simulated carbon allocation to roots following fertilization can have significant effects on pine productivity (Cropper and Gholz, 1994). Ultimately, testing the model under field conditions will help to resolve the importance of these issues.

The most appropriate models for estimating uptake and fertilizer uptake efficiency on a site-specific species-specific basis, while using this GA approach, are those that are capable of dealing with the soil chemistry of nutrient interactions in soil and nutrient movement to absorbing root surfaces. These models range from transient state to steady models that incorporate or do not incorporate inter and intra-root competition (Tinker and Nye, 2000). The models must be flexible enough to describe the changing soil fertility in a way that it reflects the nutrients capacity to move in the soil. Models with this potential, beyond the one describe here, are proposed by Luxmoore et al. (1978), De Willigen and Van Noordwijk (1987,1994a,b), Yanai (1994), Silberbush et al. (1993), Bar-Tal et al. (1991) Van Noordwijk et al. (1990), Bouldin (1989), Claaessen et al. (1986), Itoh and Barber (1983) and Barber and Cushman (1981).

Of these models, SSAND and Van Noordwijk et al. (1990) are the two that have attempted to predict fertilizer P uptake with the intent of making fertilizer recommendations. SSAND is the only one that has used the GA approach for maximizing fertilizer efficiency. For a model to do this chore properly it must handle multiple fertilizer events, allow for dynamic root growth over time, handle extramatrical mycorrhizae hyphae as well as roots, and accurately simulate P uptake and fertilizer interaction in the soil. The only one at this time that incorporates those qualities is SSAND, however all the models mentioned above have the basic theory

that would allow a version to be developed to accomplish this task and incorporate the GA approach. As an example, the Barber–Cushman model was used to successfully predict fertilizer uptake of potassium in a forest tree nursery by calculating outside the model the partitioning of potassium between the solid and solution phases to calculate a new soil solution concentration and then restart the model run at that time (Van Rees et al., 1990).

For practical applications the GA approach provides a number of significant benefits. The fitness functions can be defined in a variety of ways, allowing flexible responses to the requirements of managers. Given the high dimension problem of optimizing the addition of multiple elements at multiple dates, GA optimization should be quite efficient compared to other optimization techniques. An exhaustive exploration of the parameter space for fertilizer optimization in this study could require more than 50,000 runs of the SSAND model, assuming only six P levels for two fertilization dates. Additional runs would then be required to provide better definition of the optimum solution between the discrete fertilizer levels and dates tested. The GA technique is not likely to produce a precise estimate of the global optimum, but it is clear that efficient estimates of near optimal solutions are quite feasible. The GA approach can be coupled with systematic sampling of the parameter space around the GA optimum to evaluate parameter sensitivity and characterize the "steepness" around the optimum.

Acknowledgments

References

Adegbidi, H.G., Jokela, E.J., Comerford, N.B., Barros, N.F., 2002. Biomass development for intensively managed loblolly pine plantations growing on Spodosols in the southeastern USA. Forest Ecol. Manage. 167, 91–102.

Adegbidi, H.G., Comerford, N.B., Jokela, E.J., Barros, N.F., 2004. Root development of young loblolly pine in Spodosols in southeast Georgia. Soil Sci. Soc. Am. J. 68, 596–604.

Allen, H.L., Dougherty, P.M., Campbell, R.G., 1990. Manipulation of water and nutrients-practice and opportunity in southern U.S. pine forests. Forest Ecol. Manage. 30, 437–453.

Ball III, M.J., Hunter, D.H., Swindell, B.F., 1981. Understory biomass response to microsite and age of bedded slash pine plantations. J. Range Manage. 34, 38–42.

Barber, S.A., Cushman, J.H., 1981. Nutrient uptake model for agronomic crops. In: Iskander, I.K. (Ed.), Modelling Wastewater Renovation Land Treatment. Wiley, New York, pp. 382–409.

Bar-Tal, A., Bar-Yosef, B., Chen, Y., 1991. Validation of a model of the transport of zinc to an artificial root. J. Soil Sci. 42, 399–411.

Bouldin, D.R., 1989. A multiple ion uptake model. J. Soil Sci. 40, 309–319.

Browning, M.H.R., Whitney, R.D., 1992. The influence of phosphorus concentration and frequency of fertilization on ectomycorrhizal development in containerized black spruce and jack pine seedlings. Can. J. Forest Res. 22, 1263–1270.

Bruggeman, D.A.G., 1935. The calculation of various physical constants of heterogeneous substances. I. The dielectric constants and conductivity of mixtures composed of isotopic substances. Ann. Physik 24, 636–664.

Claaessen, N., Syringk, M., Jungk, A., 1986. Verification of a mathematical model by simulating potassium uptake from soil. Plant Soil 95, 209–220.

Colbert, S.R., Jokela, E.J., Neary, D.G., 1990. Effects of annual fertilization and sustained weed control on dry matter partitioning, leaf area, and growth efficiency of juvenile loblolly and slash pine. Forest Sci. 36, 995–1014.

Comerford, N.B., Porter, P.S., Escamilla, J.A., 1994. Application of theissen areas to models of nutrient uptake in forest ecosystems. Soil Sci. Soc. Am. J. 58, 210–215.

Conde, L.F., Swindel, B.F., Smith, J.E., 1983. Plant species cover, frequency, and biomass: early responses to clearcutting, chopping, and bedding in *Pinus elliottii* flatwoods. Forest Ecol. Manage. 6, 307–317.

Cropp, R., Gabric, A., 2002. Ecosystem adaptation: do ecosystems maximize resilience? Ecology 83, 2019–2026.

Cropper Jr., W.P., Gholz, H.L., 1994. Evaluating potential response mechanisms of a forest stand to fertilization and night temperature: a case study using *Pinus elliottii*. Ecol. Bull. (Copenhagen) 43, 154–160.

Cropper Jr., W.P., Anderson, P.J., 2004. Population dynamics of a tropical palm: use of a genetic algorithm for inverse parameter estimation. Ecol. Model. 177, 119–127.

De Willigen, P., Van Noordwijk, M., 1987. Uptake potential of non-regularly distributed roots. J. Plant Nutr. 10, 1273–1280.

De Willigen, P., Van Noordwijk, M., 1994a. Diffusion and mass flow to a root with constant nutrient demand or behaving as a zero-sink. 1. Constant uptake. Soil Sci. 157, 162–170.

De Willigen, P., Van Noordwijk, M., 1994b. Diffusion and mass flow to a root with constant nutrient demand or behaving as a zero sink. 2. Zero sink. Soil Sci. 157, 171–175.

Gholz, H.L., Fisher, R.F., Pritchett, W.L., 1985. Nutrient dynamics in slash pine plantation ecosystems. Ecology 66, 647–659.

Grierson, P.F., Comerford, N.B., Jokela, E.J., 1999. Phosphorus mineralization and microbial biomass in a Florida Spodosol: effects

of water potential, temperature and fertilizer application. Biol. Fertil. Soils 28, 244–252.

Ibriki, H., Comerford, N.B., Hanlon, E.A., Rechcigl, J.E., 1994. Phosphorus uptake by bahiagrass from Spodosols: observations and modeling of uptake from different horizons. Soil Sci. Soc. Am. J. 58, 139–143.

Itoh, S., Barber, S.A., 1983. A numerical solution of whole plant nutrient uptake for soil root systems with root hairs. Plant Soil 70, 403–413.

Jokela, E.J., Martin, T.A., 2000. Effects of ontogeny and soil nutrient supply on production, allocation and leaf area efficiency in loblolly and slash pine stands. Can. J. Forest Res. 30, 1511–1524.

Kelly, J.M., Ericsson, T., 2003. Assessing the nutrition of juvenile hybrid poplar using a steady state technique and a mechanistic model. Forest Ecol. Manage. 180, 249–260.

Koza, J.R., Keane, M.A., Streeter, M.J., 2003. Evolving inventions. Sci. Am. 288, 52–59.

Luxmoore, R.J., Begovich, C.L., Dixon, K.R., 1978. Modelling solute uptake and incorporation into vegetation and litter. Ecol. Model. 5, 137–171.

Mitchell, M., Taylor, C.E., 1999. Evolutionary computation: an overview. Annu. Rev. Ecol. Systematics 30, 593–616.

Nye, P.H., Tinker, P.B., 1997. Solute Movement in the Soil-Root System. University of California Press, Berkeley, 342 pp.

Phillips, L.R., Comerford, N.B., Neary, D.G., Mansell, R.S., 1989. Distribution and simulation of soil water above a shallow, fluctuating water table in a forested Spodosol. Soil Sci. Soc. Am. J. 53, 1236–1241.

Polglase, P.J., Comerford, N.B., Jokela, E.J., 1992. Mineralization of nitrogen and phosphorus from soil organic matter in southern pine plantations. Soil Sci. Soc. Am. J. 56, 921–927.

Pritchett, W.L., Llewellyn, W.R., 1966. Response of slash pine to phosphorus in sandy soils. Soil Sci. Soc. Am. Proc. 30, 509–519.

Silberbush, M., Sorek, S., Yakirevich, A., 1993. K^+ uptake by root systems grown in soils under salinity. I. A mathematical model. Transport Porous Media 11, 101–116.

Smethurst, P.J., 1992. Application of solute transport theory to predict uptake of K and P by competing slash pine and grass. Ph.D. dissertation, University of Florida, 180 pp.

Smethurst, P.J., Comerford, N.B., 1993. Simulating nutrient uptake by single or competing and contrasting root systems. Soil Sci. Soc. Am. J. 57, 1361–1367.

Smethurst, P.J., Comerford, N.B., Neary, D.G., 1993a. Predicting the effects of weeds on K and P uptake by young slash pine on a Spodosol. Forest Ecol. Manage. 60, 27–39.

Smethurst, P.J., Comerford, N.B., Neary, D.G., 1993b. Weed effects on early K and P nutrition and growth of slash pine on a Spodosol. Forest Ecol. Manage. 60, 15–26.

Tianhong, L., Yanxin, S., An, X., 2003. Integration of large scale fertilizing models with GIS using minimum unit. Environ. Model. Software 18, 221–229.

Tinker, P.B., Nye, P.H., 2000. Solute Movement in the Rhizosphere. Oxford University Press, Oxford, UK.

Van Noordwijk, M., De Willigen, P., Ehlert, P.A.I., Charden, W.J., 1990. A simple model of P uptake as a possible basis for P fertilizer recommendations. Neth. J. Agric. Sci. 38, 317–332.

Van Rees, K.C.J., Comerford, N.B., McFee, W.W., 1990. Modeling potassium uptake by slash pine seedlings from low potassium supplying soils of the southeastern coastal plain. Soil Sci. Soc. Am. J. 54, 1413–1421.

Williams, M., Yanai, R.D., 1996. Multi-dimensional sensitivity analysis and ecological implications of a nutrient uptake model. Plant Soil 180, 311–324.

Wilson, W., 2000. Simulating Ecological and Evolutionary Systems in C. Cambridge University Press, Cambridge, UK.

Yanai, R.D., 1994. A steady-state model of nutrient uptake accounting for newly grown roots. Soil Sci. Soc. Am. J. 58, 1562–1571.