

Analyzing the functional type concept in arctic plants using a dynamic vegetation model

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Grouping organisms into categories based on common traits has been a tool of ecological scientists for some time now. Defining groups of species, examples being life forms and functional types, is an operational procedure, conducted to answer a particular question. This becomes rather practical when performing analyses at coarse spatial scales, given data limitations and the potential for species redundancy. However, the implications of aggregating organisms for modeling purposes are still unclear. Does averaging the traits of several species into a functional type sufficiently represent the dynamics of the individual components? How much variability is lost when we aggregate species into groups? In an attempt to address these questions, we examined how the level of vegetation aggregation affected a variety of ecosystem properties using a regional-scale model of arctic tundra ecosystems (ArcVeg). We used four levels of aggregation: species (15 dominant ones), functional types (7), life forms (4) and vegetation type (1), in addition to two methods of aggregation (simple vs weighted means of plant parameter values). We found that the level of aggregation consistently affected community composition, total community biomass and ecosystem net primary production (NPP). Neither simple means nor weighted means of aggregated parameter values adequately captured the ecosystem properties simulated at lower levels of aggregation. Aggregation of vegetation (i.e. reduced parameter variability) using simple means underestimated total biomass, whereas aggregation using weighted means overestimated total biomass. Aggregation led to increases in NPP with both methods. These findings suggest that aggregating vegetation, particularly to levels less detailed than plant functional types, will have important implications for regional-scale modeling of vegetation dynamics and carbon cycling.

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Grouping organisms into categories based on common structural and functional traits, irrespective of phylogeny, is a tool that ecologists have long used to generalize about properties of ecosystems (Gitay and Noble 1997, Shugart 1997, Díaz et al. 1998). Classification systems for these groupings include, but are not limited to, life forms (Raunkiaer 1934), guilds (Root 1967) and functional types (classifica-

tions based on species responses to environmental factors, e.g. Cummins 1974, Keddy 1992). A current need for defining groups of organisms, such as functional types, in plant and ecosystem ecology has arisen from the attempt to understand vegetation and ecosystem dynamics over large areas in response to global change (Chapin 1993, Dawson and Chapin 1993).

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Early biogeographic models of vegetation distribution assumed equilibrium between plants and their environment. These models use present vegetation-environment relationships to predict shifts of vegetation types in response to environmental changes (e.g. Holdridge 1947, Whittaker 1975, Prentice et al. 1992). While these models provide plausible patterns of vegetation change, they fail to capture the transient dynamics that occur because of time lags in plant response and migration (Starfield and Chapin 1996, Woodward and Beerling 1997). In addition, short-term field experiments (several years) (Lauenroth et al. 1978, Chapin and Shaver 1985, Arft et al. 1999) and long-term pollen records (Davis 1981, Brubaker et al. 1995) indicate that species respond individually to changes in the environment, so shifts of entire units of vegetation are unlikely to occur.

In order to capture the individualistic nature of species responses, models that simulate transient dynamics of species are necessary; however, there are practical limitations regarding the collection and analysis of data on all species (Steffen et al. 1992, Smith et al. 1993, Kittel et al. 2000). Species-level data may also not be necessary, if several species are similar with respect to the functions of interest (MacArthur 1955, Walker 1992, Lawton and Brown 1993, Rastetter and Shaver 1995, Johnson et al. 1996, Sullivan and Zedler 1999). Plant functional types are used as a compromise that allows important functional attributes of individual species to be aggregated while still considering the heterogeneity of vegetation (Woodward and Beerling 1997). Rastetter et al. (1992) describe this method of aggregation (from fine to coarse scales) as “partitioning” the variance. Currently, not many regional- to global-scale models of ecosystem dynamics employ this technique; most coarse-scale biogeochemical models operate at the level of total vegetation or separate vegetation into only a few broad categories (e.g. McGuire et al. 1995, McKane et al. 1997).

In practice, defining functional types is an operational procedure, conducted to achieve a specific goal or to answer a particular question (Gitay and Noble 1997). While there may be no single, comprehensive set of functional types, developing subjective, user-defined classifications of organisms has been a valuable approach for examining ecosystem responses to environmental gradients or changes (e.g. Diamond 1975, Noble and Slatyer 1980, Chapin 1993, Aguiar et al. 1996, Paruelo and Lauenroth 1996). Recently some methods have been developed for more objective groupings of species into functional types (Chapin et al. 1996, Hodgson et al. 1999).

Despite the practical need for using functional types in modeling efforts, there have been few explicit tests of the concept (see Rastetter et al. 1992, Rastetter and Shaver 1995, Smith 1997), and many questions remain unanswered. The simplification of the system using

functional types still makes the assumption that responses of individual species can be generalized (Chapin 1993, Smith et al. 1993). Under what conditions does the averaging of traits across several species into functional types adequately predict the behavior of the system? What level of aggregation in the plant community is appropriate for representing the important vegetation and ecosystem dynamics at a particular spatial scale? How much variability in ecosystem performance is lost when we aggregate species into groups? As a step toward addressing these questions, we conducted a study using a dynamic vegetation model (ArcVeg; Epstein et al. 2000) to simulate tundra vegetation at varying levels of aggregation. Our main objective for this effort was to determine how the level of aggregation in tundra vegetation affected the simulation of ecosystem properties, such as species composition, total biomass, and net primary production (NPP).

Methods

ArcVeg model of tundra dynamics

We used a dynamic vegetation model of arctic tundra (ArcVeg; see Epstein et al. 2000 for a complete description) to examine the effects of aggregating vegetation when simulating arctic ecosystems. The model is based on a simple, mass-balance nitrogen (N) cycle (Fig. 1). Arctic tundra systems are generally nitrogen-limited, where plants compete for available nitrogen and respond rather quickly to additions of nitrogen (Shaver et al. 1992, Shaver and Chapin 1995, Schimel et al. 1996). ArcVeg is currently parameterized for moist, acidic systems and has been used by Epstein et al. (2000) to simulate the dynamics of high arctic and low arctic moist acidic tundra (*sensu* Bliss and Matveyeva 1992).

ArcVeg is unique in that it contains a sufficient level of detail to run at various levels of aggregation using functional groupings of plants. ArcVeg currently simu-

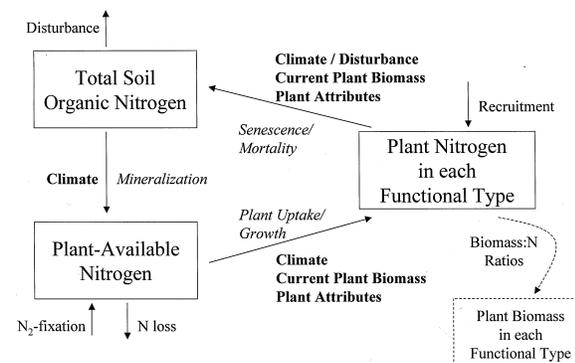


Fig. 1. ArcVeg flow diagram. Model pools are in boxes. The main processes are in italics next to the arrows, and the controls on these processes are in bold next to the arrows.

lates up to 15 tundra “plant types”, which represent a combination of species, genera and plant functional types. These plant types are high arctic forbs, low arctic forbs, *Equisetum* spp., *Eriophorum* spp., *Carex* spp., grasses and other monocots, *Cassiope* and *Empetrum* spp., *Ledum* spp., *Vaccinium* spp. (evergreen), *Dryas* spp., *Salix* spp., *Betula* spp., *Alnus* spp., mosses, and lichens (Table 1). Many of the plant types parameterized at the genus level actually represent a single important species (e.g. *Betula nana* for *Betula* spp.). The model runs on an annual time step to simulate transient, interannual dynamics, and it can be run for up to 100 independent patches (1 m² each) of vegetation to represent spatial heterogeneity of a landscape. Each plant type in the model is parameterized for five traits based on field data (Table 1): 1) mean biomass:nitrogen ratio for the whole plant (g biomass/g N), 2) proportion of biomass senescing at the end of the growing season (g/g), 3) annual probability of establishment of new individuals, 4) nitrogen uptake efficiency (g N taken up/g biomass), 5) timing of growth and cold-tolerance. Together these attributes represent a variety of strategies for plant growth and survival.

Modeling approach

We conducted two separate analyses. The first analysis was designed to examine the sensitivity of the model output to plant attribute variability within a plant functional type. Based on the initial parameterization of the model, from data found in the literature (see Epstein et al. 2000), the deciduous shrub functional type had the greatest variation among species in plant attributes. The deciduous shrub type, with its component species, *Salix (pulchra)*, *Betula (nana)* and *Alnus (crispa)*, is therefore the most appropriate functional type for conducting this analysis. In the initial parameterization of the model, *Salix*, *Betula* and *Alnus* have similar nutrient uptake efficiencies and probabilities of establishment, yet they differ with regard to the three other plant attributes. We therefore focus on these three parameters (mean biomass:N ratio, proportion of biomass senescing, and timing of growth) to differentiate species within the functional type of deciduous shrubs.

Proportion of biomass senescing is a rather straightforward parameter; however, biomass:N ratio and tim-

Table 1. Plant types and associated model parameters (data from Epstein et al. 2000). Values are simple means; weighted means that differ from simple means are in parentheses.

Aggregation level***	Average biomass:nitrogen ratio (g biomass/g N)	Proportion of biomass senescing (yr ⁻¹)	Nutrient uptake efficiency (g N/g biomass)*	Probability of establishment (yr ⁻¹)	Growing season requirements (min. PGP)**
Whole plant community (VT)	93 (102)	0.26 (0.16)	0.0300	0.30	2
Non-vascular (LF)	165 (146)	0.08 (0.09)	0.0012	0.35	1
Moss (FT, SP)	130	0.10	0.0018	0.50	1
Lichen (FT, SP)	200	0.05	0.0006	0.20	1
Forb (LF, FT)	42 (43)	0.53 (0.54)	0.0400	0.50	1
High Arctic acid	40	0.55	0.0400	0.50	1
Low Arctic acid	40	0.50	0.0400	0.50	1–2
<i>Equisetum</i> spp.	45	0.55	0.0400	0.50	1
Graminoids (LF)	72 (70)	0.35 (0.31)	0.0350	0.33	2
Sedge (FT)	70	0.33 (0.30)	0.0350	0.25	2
<i>Eriophorum</i> spp.	70	0.30	0.0350	0.25	2
<i>Carex</i> spp.	70	0.35	0.0350	0.25	2
Grass (FT, SP)	75	0.40	0.0350	0.50	2
Shrubs (LF)	94 (88)	0.16	0.0325	0.19	3
Deciduous shrub (FT)	88 (80)	0.16 (0.17)	0.0350	0.20	3
<i>Salix</i> spp.	65	0.20	0.0350	0.20	2–3
<i>Betula</i> spp.	90	0.15	0.0350	0.20	3
<i>Alnus</i> spp.	110	0.13	0.0350	0.20	4
Evergreen shrub (FT)	99 (100)	0.16 (0.15)	0.0300	0.19	3
<i>Cassiope</i> and <i>Empetrum</i>	100	0.15	0.0300	0.20	3
<i>Ledum</i> spp.	100	0.15	0.0300	0.10	3
<i>Vaccinium</i> spp.	100	0.15	0.0300	0.20	3
<i>Dryas</i> spp.	95	0.17	0.0300	0.25	3

* Varies throughout growing season [N uptake efficiency is zero during plant growth periods (PGPs) below the minimum required for that plant type]. See text for explanation.

** Minimum PGP for plant growth to occur (during PGPs below this value, the plant type does not take up nitrogen); the lower the value the greater the cold-tolerance of the plant type.

*** Aggregation level for the various simulations – note that some groupings are used at more than one aggregation level: (VT = vegetation type; LF = life form; FT = functional types; SP = “species”; no label is species only).

ing of growth require additional explanation. Biomass:N ratio in ArcVeg is parameterized on a whole plant level, based on N concentrations for different tissue types weighted by the biomass of tissue types for a mature plant. An assumption here is that the N concentrations of net primary production and senesced tissue are equivalent. While this may be a reasonable assumption for many of the plant functional types simulated (e.g. mosses, lichens, graminoids), the N concentrations of senescing material of woody plants (i.e. mainly foliage and fine roots) may be greater than those of the plant as a whole. High N resorption by shrubs, however, may make the N concentrations of senesced tissue more comparable to those of the slower turnover woody tissue (e.g. Berendse and Jonasson 1992).

In order to simulate timing of growth, we split the growing season into discrete plant growth periods (PGPs). PGPs can be thought of as temperature-related time periods within a growing season, with the coldest (earliest) part of the growing season being PGP(1) and each successive PGP having maximum temperatures greater than the prior one. The model includes a set of probabilities for the occurrence of each PGP in a given year, such that PGP(1) always occurs, and the occurrence of PGP(i) is conditional on the occurrence of PGP($i - 1$), with a maximum of 5 PGPs. The final PGP in a given year encompasses the time of peak temperatures and includes the remainder of the growing season. Therefore, we can simulate a relatively cold, short growing season (maximum PGP of 1) or a relatively warm, long growing season (maximum PGP of 5). Activity of a plant type during a PGP is determined by its nutrient uptake efficiency. For example, all shrubs have nutrient uptake efficiency of zero during PGP 1, meaning that they are not active at the very earliest part of the growing season (*Salix* spp. is the shrub type with the earliest activity – PGP 2). To alter the timing of growth for a plant type or species we vary the nutrient uptake efficiencies in certain PGPs. For a more complete description of this construct, see Epstein et al. 2000.

For our second analysis, we examined the effects of aggregation on simulations of plant community composition, total biomass, and net primary production. We simulated the predominant plant community of moist-acidic, low arctic tundra at four hierarchical levels of aggregation; these levels, from least to most aggregated, were “species”, “functional types”, “life forms” and “vegetation type” (i.e. fully aggregated). At the species level, all 15 of the plant types were parameterized uniquely for the model (Table 1). At the functional type level, we derived seven groups (mosses, lichens, forbs, sedges, grasses, deciduous shrubs, and evergreen shrubs) from the original 15 plant types by averaging the parameter values across the components of each functional type. We again averaged parameter values to derive four life forms (non-vascular, forbs, graminoids,

and shrubs), and at the most aggregated level, the vegetation type of low arctic, moist acidic tundra was represented by parameter values averaged across all fifteen plant types. For each aggregation level, we ran two sets of simulations using different averaging methods – one with a simple average of parameter values across component plant types, the other using a weighted average of parameter values, based on observed abundances of plant types in moist acidic, low arctic tundra (data from Epstein et al. 2000).

Simulating vegetation patterns

For our first analysis, we used ArcVeg to examine the effects of plant attribute variability within a functional type on community composition, biomass, and NPP of the low arctic tundra ecosystem. For this analysis we focused on the aggregation of the plant community into the seven plant functional types (mosses, lichens, forbs, grasses, sedges, deciduous shrubs, evergreen shrubs). The one exception was that the deciduous shrubs were composed of three separate species (*Salix*, *Betula*, *Alnus*), that differed in the values of the three parameters of interest (biomass:N ratio, proportion of biomass senescing, timing of growth). We focused on each parameter singly (i.e. varied one parameter while holding the other two parameters constant across the three species). In all cases, the mean value of each parameter across the deciduous shrub functional type remained constant; only the variance was altered for each simulation (Table 2). For example, biomass:N ratio of the deciduous shrub functional type was assumed to be constant at 88 g biomass/g N (Babb and Whitfield 1977, Tieszen et al. 1981, Hobbie 1996). We ran four sets of simulations; the first had each deciduous shrub species (*Salix*, *Betula*, *Alnus*) parameterized at 88 g biomass/g N. In the second simulation biomass:N ratio was parameterized at 92 g biomass/g N for *Alnus*, 88 g biomass/g N for *Betula* and 84 g biomass/g N for *Salix*. We altered *Alnus* and *Salix* biomass:N ratios to 96 and 80 g biomass/g N, respectively for the third simulation, and to 100 and 76 g biomass/g N, respectively for the fourth simulation.

We conducted a similar set of model runs for the proportion of biomass senescing parameter (Table 2). For an analysis of the timing of growth parameter, we extended the nutrient uptake capability (i.e. nutrient uptake efficiency parameter) of *Salix* into an earlier growth period (PGP 2) and reduced the nutrient uptake capability of *Alnus* during the usual start of the growing season for deciduous shrubs (PGP 3). The total number of model executions for this analysis was therefore ten – one for the baseline parameter set (used for all three parameters of interest) and three executions that had variable parameter values for *Salix*, *Betula*, and *Alnus* for each of three plant attributes.

Table 2. Sets of deciduous shrub species parameters for different model executions.

Execution no.	Average biomass:nitrogen ratio (g biomass/g N)		Proportion of biomass senescing (yr ⁻¹)		Timing of growth: nutrient uptake efficiencies in growth periods 2–4 (g N/g biomass)									
	1	2	3	4	1	5	6	7	1	8	9	10		
Plant species														
<i>Salix</i>	88	84	80	76	0.16	0.17	0.18	0.19	0.000; 0.035; 0.035	0.001; 0.035; 0.035	0.003; 0.035; 0.035	0.003; 0.035; 0.035		
<i>Betula</i>	88	88	88	88	0.16	0.16	0.16	0.16	0.000; 0.035; 0.035	0.000; 0.035; 0.035	0.000; 0.035; 0.035	0.000; 0.035; 0.035		
<i>Alnus</i>	88	92	96	100	0.16	0.15	0.14	0.13	0.000; 0.035; 0.035	0.000; 0.034; 0.035	0.000; 0.033; 0.035	0.000; 0.032; 0.035		
Mean	88	88	88	88	0.16	0.16	0.16	0.16	0.000; 0.035; 0.035	0.000; 0.035; 0.035	0.000; 0.035; 0.035	0.000; 0.035; 0.035		
SD	0	4	8	12	0	0.01	0.02	0.03	0.000	0.001	0.002	0.003		

In a preliminary analysis of model output stochasticity, we found that means for total biomass and net primary production were converged upon after approximately 20 repeated simulations, and constant variances were reached after approximately 40 simulations. Each of the ten model executions described above therefore consisted of 40 separate simulations of the model for 1000 yr and 100 spatially independent patches (1 m² each), starting at zero total biomass. Differences among model simulations are a result of temporally stochastic variation in climate (i.e. the number of PGPs varies among years) and disturbance in the model, in addition to patch-level stochasticity (e.g. fine-scale disturbances such as frost scars, and establishment of new individuals). Biomass and NPP for each plant functional type (and each deciduous shrub species) were calculated by averaging across the 100 patches for the last 200 yr of each 1000-yr simulation. This ensures that the model has reached a stochastic equilibrium plant community (after 800 yr) and incorporates interannual variability into the mean. We then calculated mean community biomass and NPP values, in addition to mean biomass for each functional type and deciduous shrub species, with standard errors across the 40 model runs. Because we used the minimum number of model runs for which the variance among runs is accurately represented (40), the standard error is not confounded by an artificially high number of observations (n) and is effectively a conservative estimate for comparing variability across model treatments. We consider model treatments to be different when standard errors do not overlap.

For our second analysis, we used ArcVeg to simulate the plant community composition, biomass, and NPP of a typical low arctic tundra ecosystem at four different levels of aggregation, with two different averaging methods (Table 1). As described above each of the seven model executions (the 15-“species” baseline run plus three levels of aggregation using each of two averaging methods) consisted of 40 separate simulations of the model for 1000 yr and 100 spatially independent patches (1 m² each), starting at zero total biomass. Biomass and NPP for each plant grouping were again calculated by averaging across the 100 patches for the last 200 yr of each 1000-yr simulation to ensure that the model has reached a stochastic equilibrium plant community. We then calculated mean biomass and NPP values with standard errors for each plant grouping across the 40 model runs.

Results

Sensitivity analysis

In all cases, variation in plant attributes at the species level (within the deciduous shrub functional type) led to changes in community composition, total biomass and

NPP at the functional-type level, even though mean values for functional type parameters were held constant. Changes in biomass:N ratio of $\pm 4.5\%$, $\pm 9.1\%$ and $\pm 13.6\%$ for *Alnus* and *Salix* (with the mean value remaining at 88), respectively, led to a maximum increase of 45% (difference in mean values from the base scenario) in deciduous shrub biomass (as a result of an increase in *Alnus* biomass) and a 47% maximum reduction in evergreen shrub biomass (Fig. 2a, b). Total biomass of the plant community increased from 1186 g m⁻² to 1279 g m⁻² with increased variability in biomass:N ratio among the deciduous shrubs (Fig. 2c). NPP increased from 203 g m⁻² yr⁻¹ to 214 g m⁻² yr⁻¹ with changes in biomass:N ratio at the species level (Fig. 2d).

Some similar results were found with regard to variation in proportion of biomass senescing. Changes of $\pm 6.3\%$, $\pm 12.5\%$ and $\pm 18.8\%$ for *Salix* and *Alnus* (with the mean value remaining at 0.16) led to a 59% maximum increase in deciduous shrub biomass (again as a result of an increase in *Alnus* biomass) and a 53% reduction in evergreen shrub biomass (Fig. 3a, b). Total plant community biomass increased from 1186 g m⁻² to 1301 g m⁻² with increased variability in proportion senescing among deciduous shrubs (Fig. 3c). NPP did not vary with changes in proportion senescing at the species level (Fig. 3d).

Changes in the timing of growth at the species level also led to compositional and total biomass changes at the functional-type level. By allowing *Salix* to take up nitrogen earlier in the growing season and restricting

some of the nitrogen uptake of *Alnus* until later in the growing season, we simulated a 74% increase in deciduous shrub biomass. Concomitant with this increase in deciduous shrub biomass were decreases of 52% in evergreen shrub biomass and 49% in graminoid biomass (Fig. 4a). The increase in deciduous shrub biomass was due to a greater than four-fold increase in *Salix* biomass (Fig. 4b). Total plant community biomass increased from 1186 g m⁻² yr⁻¹ to 1297 g m⁻² yr⁻¹ with increased variability in timing of growth among deciduous shrubs (Fig. 4c). NPP did not vary with changes in timing of growth at the species level (Fig. 4d).

Aggregation analysis – simple means

Varying the level of aggregation for the tundra vegetation (using simple means of parameter values) affected the simulated species composition, total biomass and net primary production of these ecosystems at equilibrium. Aggregating the vegetation from 15 “species” to seven functional types almost doubled the contribution of sedges to community biomass (88 g m⁻² and 7% of community biomass to 162 g m⁻² and 14% of community biomass) and altered the percent composition of evergreen shrubs from 24% to 20% (Fig. 5a). The greatest effect of an additional aggregation to four life forms was to increase non-vascular plant biomass from 342 g m⁻² (29% of community biomass) at the functional-type level to 534 g m⁻² (38% of community

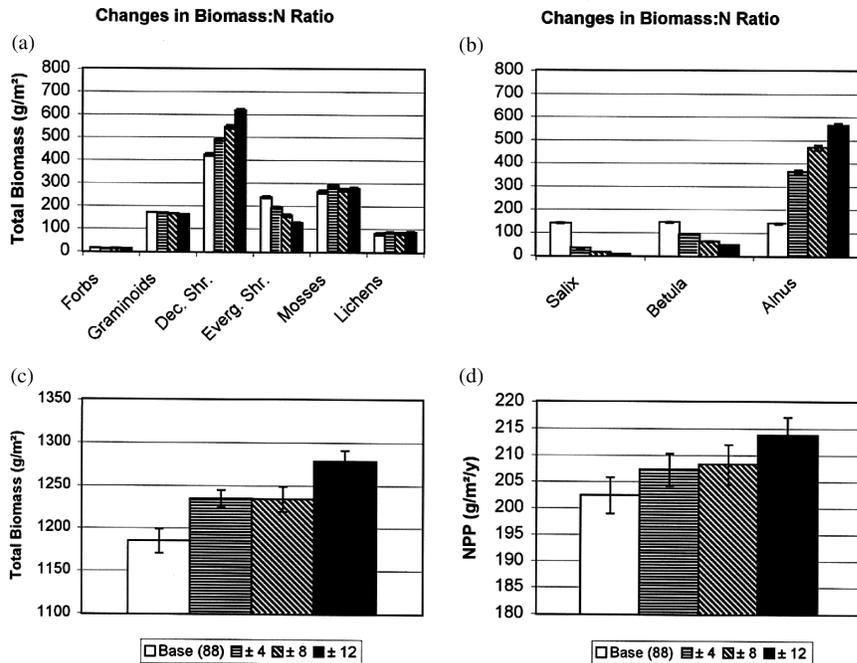


Fig. 2. Effects of increased variability in biomass:N ratio of deciduous shrubs on a) total biomass (above- plus belowground in g m⁻²) of seven plant functional types, b) total biomass of the three deciduous shrub species, c) total biomass of the entire plant community, and d) net primary production (above- plus belowground in g m⁻² yr⁻¹). Data are means \pm standard error, $n = 40$ replicate simulations (data for each replicate simulation are means across 200 yr and 100 patches).

biomass) at the life-form level (Fig. 5b). Total community biomass was variable across aggregation levels, particularly between the life-form level (1390 g m^{-2}) and the vegetation-type level, where all plant species were combined (830 g m^{-2}) (Fig. 5c).

The effect of aggregation on NPP was similar to that described for biomass, except at the highest level of aggregation. Simulated NPP of sedges increased from $27 \text{ g m}^{-2} \text{ yr}^{-1}$ to $53 \text{ g m}^{-2} \text{ yr}^{-1}$ when aggregating from the species level to the functional-type level, and NPP of both deciduous and evergreen shrubs decreased with this aggregation (Fig. 6a). The greatest effect of the aggregation to the life-form level was to increase non-vascular NPP from $30 \text{ g m}^{-2} \text{ yr}^{-1}$ (functional-type aggregation) to $43 \text{ g m}^{-2} \text{ yr}^{-1}$ (Fig. 6b). Total community NPP increased approximately 10% from the two least aggregated scenarios to the two most aggregated scenarios (Fig. 6c), whereas biomass decreased at the highest level of aggregation.

Aggregation analysis – weighted means

Varying the level of aggregation using weighted means of parameter values also affected the simulated species composition, total biomass and net primary production of low arctic tundra. Aggregating the vegetation from 15 “species” to seven functional types more than doubled the biomass of sedges (88 g m^{-2} and 7% of community biomass to 198 g m^{-2} and 16% of community biomass) and evergreen shrubs (306 g m^{-2} and 24% to 702 g m^{-2} and 55%), and made deciduous

shrubs a very minor part of the plant community (Fig. 7a). An additional aggregation to four life forms decreased shrub biomass from 731 g m^{-2} at the functional-type level to 535 g m^{-2} at the life-form level, and decreased non-vascular biomass from 331 g m^{-2} to 170 g m^{-2} (Fig. 7b). Total community biomass was again variable across aggregation levels, particularly between the life-form level (974 g m^{-2}) and the vegetation-type level, where all plant species were combined (1511 g m^{-2}) (Fig. 7c).

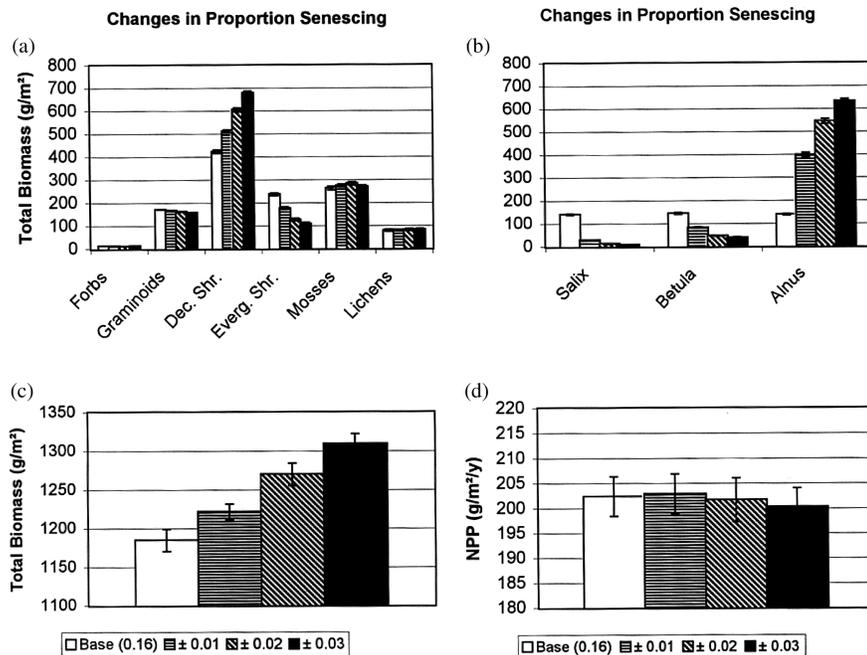
Simulated NPP of sedges increased from $27 \text{ g m}^{-2} \text{ yr}^{-1}$ to $65 \text{ g m}^{-2} \text{ yr}^{-1}$ when aggregating from the species level to the functional-type level. NPP of evergreen shrubs increased from $46 \text{ g m}^{-2} \text{ yr}^{-1}$ to $112 \text{ g m}^{-2} \text{ yr}^{-1}$, while NPP of deciduous shrubs decreased to only $5 \text{ g m}^{-2} \text{ yr}^{-1}$ (Fig. 8a). Aggregation to the life-form level decreased non-vascular NPP from $30 \text{ g m}^{-2} \text{ yr}^{-1}$ (functional-type aggregation) to $14 \text{ g m}^{-2} \text{ yr}^{-1}$ (Fig. 8b). Total NPP for the single vegetation-type scenario was essentially double that of any other aggregation scenario (Fig. 8c).

Discussion

Effects of plant parameters on simulated ecosystem properties

Aggregating vegetation in ArcVeg, a plant community and ecosystem dynamics model, does alter the simulated community composition, total biomass, and net primary production. However, it is important to under-

Fig. 3. Effects of increased variability in proportion of biomass senescing for deciduous shrubs on a) total biomass (above- plus belowground in g m^{-2}) of seven plant functional types, b) total biomass of the three deciduous shrub species, c) total biomass of the entire plant community, and d) net primary production (above- plus belowground in $\text{g m}^{-2} \text{ yr}^{-1}$). Data are means \pm standard error, $n = 40$ replicate simulations (data for each replicate simulation are means across 200 yr and 100 patches).



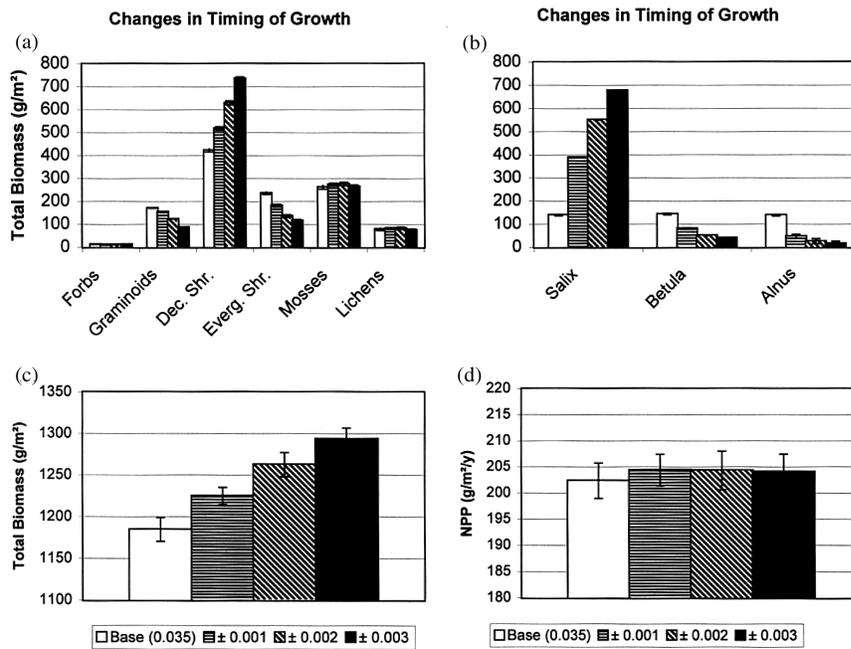


Fig. 4. Effects of increased variability in timing of growth for deciduous shrubs on a) total biomass (above- plus belowground in g m^{-2}) of seven plant functional types, b) total biomass of the three deciduous shrub species, c) total biomass of the entire plant community, and d) net primary production (above- plus belowground in $\text{g m}^{-2} \text{ yr}^{-1}$). Data are means \pm standard error, $n = 40$ replicate simulations (data for each replicate simulation are means across 200 yr and 100 patches).

stand the effects of variation in plant parameters on these system properties (biomass, NPP and community composition) in the model, before evaluating the results of our analyses. A key assumption of the model is that plant available nitrogen is the single limiting resource for primary production. NPP for a plant type is calculated as the mass of nitrogen taken up ($\text{g N m}^{-2} \text{ yr}^{-1}$) times the biomass:N ratio ($\text{g biomass g}^{-1} \text{ N}$) of the plant. The biomass of a plant type in the model is at equilibrium when NPP equals the annual rate of senescence. The maximum equilibrium biomass of a plant type, assuming that the plant type acquires all of the available nitrogen (i.e. a monoculture and no N loss), therefore occurs when

$$\text{N available} \times \text{biomass:N ratio} = (\text{N available} \times \text{biomass:N ratio} + \text{BIOMASS}) \times \text{proportion senescing} \quad (1)$$

Solving for biomass,

$$\text{Max. BIOMASS} = (\text{N available} \times \text{biomass:N ratio}) / \text{proportion senescing} - \text{N available} \times \text{biomass:N ratio} \quad (2)$$

Substituting NPP for $\text{N available} \times \text{biomass:N ratio}$

$$\text{Max. BIOMASS} = \text{NPP} / \text{proportion senescing} - \text{NPP}, \text{ or}$$

$$\text{Max. BIOMASS} = \text{NPP} \times (1 / \text{proportion senescing} - 1) \quad (3)$$

Based on these equations, NPP is directly related to plant biomass:N ratio, whereas biomass is related to both biomass:N ratio and proportion senescing. N uptake by a plant type, however, is not likely to be the total available N pool. Plants compete for N in the model based on three factors: current biomass, N uptake efficiencies and timing of growth, the latter allowing for a temporal partitioning of resources (N). Because competition in ArcVeg is a function of biomass and varies intraseasonally, plant community composition is influenced by all three plant parameters included in our sensitivity analysis (biomass:N ratio, proportion senescing and timing of growth).

Due to the limiting nature of N in the model, the plant community will essentially take up the entire plant-available N pool (the exception being recently disturbed patches with low plant biomass). Therefore the total amount of N in community NPP is rather consistent across model simulations where disturbance and climate are unchanged. The one parameter that will have an effect on N sequestered in plant biomass is turnover time (proportion senescing) of the plants in the community. Because the soil organic pool of N is large relative to the amount in live biomass, N sequestered in live plants will have a very minor influence on N mineralized and the resultant NPP.

Sensitivity analysis

Sensitivity analyses of individual plant parameters illustrate the effects of parameter variability on the ecosys-

tem attributes of total biomass, NPP and community composition. Increasing the variability of the biomass:N ratio parameter among deciduous shrubs affected all three of these ecosystem attributes. The individual species with the greatest biomass:N ratio (in this case *Alnus*, which has a large proportion of low-N woody tissue), dominated among the deciduous shrubs. This dominance of a species with a high biomass:N ratio led to an increase in total NPP, since NPP in ArcVeg is the product of N uptake and biomass:N ratio. The increase in NPP, with proportion of biomass senescing held constant, increased total community biomass, and the increase in deciduous shrub biomass led to a decrease in evergreen shrub biomass as a result of competition for N.

Increasing the variability in the proportion of biomass senescing parameter influenced both total community biomass and community composition. The individual species with the smallest proportion of biomass senescing (again *Alnus*, because of the large proportion of low-turnover woody tissue) dominated among the

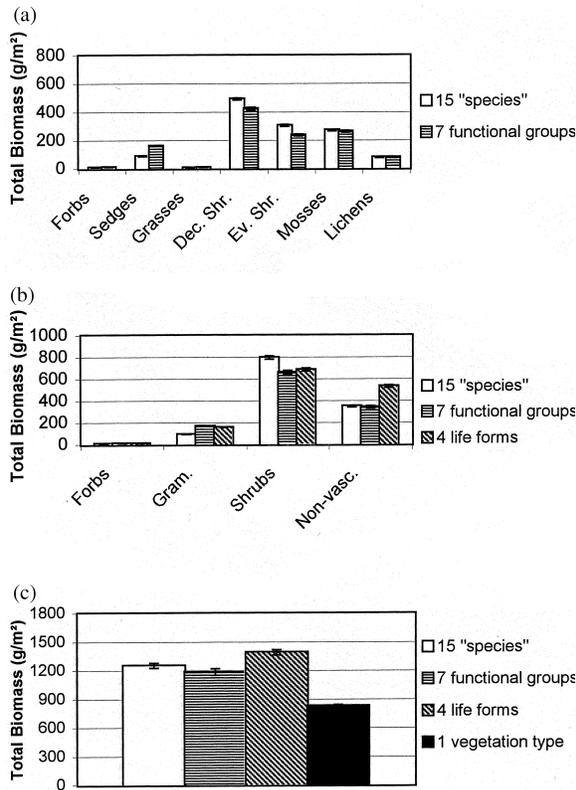


Fig. 5. Total plant biomass (above- plus belowground in g m^{-2}) for a) seven plant functional types at two levels of aggregation, b) four life forms at three levels of aggregation, and c) the entire plant community at four levels of aggregation, using simple means for averaging parameter values. Data are means \pm standard error, $n = 40$ replicate simulations (data for each replicate simulation are means across 200 yr and 100 patches).

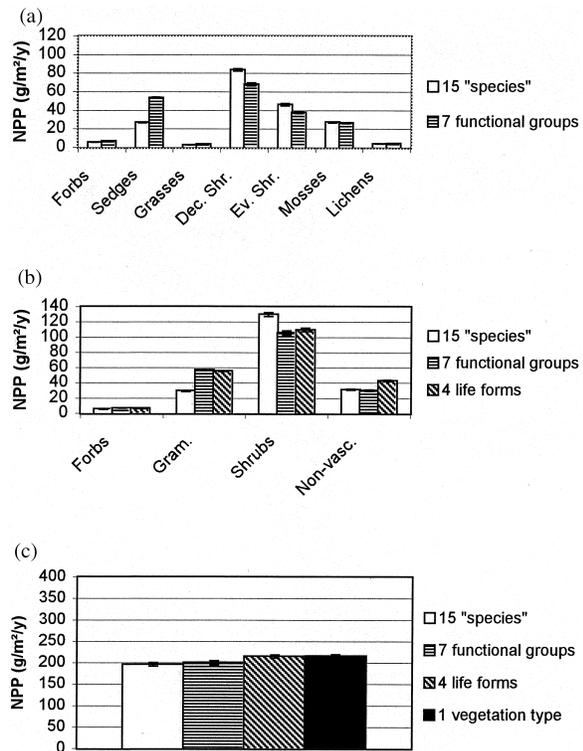


Fig. 6. Net primary production (above- plus belowground in $\text{g m}^{-2} \text{yr}^{-1}$) for a) seven plant functional types at two levels of aggregation, b) four life forms at three levels of aggregation, and c) the entire plant community at four levels of aggregation, using simple means for averaging parameter values. Data are means \pm standard error, $n = 40$ replicate simulations (data for each replicate simulation are means across 200 yr and 100 patches).

deciduous shrubs. This did not elicit changes in ecosystem NPP, since NPP in the model is calculated independently from proportion of biomass senescing. However, total community biomass increased with greater variability in the proportion of biomass senescing parameter, because the dominant species had the slowest tissue turnover rate and was therefore able to accumulate greater quantities of biomass. Again deciduous shrubs outcompeted evergreen shrubs for available N.

Increasing the variability of timing of growth among the deciduous shrubs also influenced total community biomass and community composition. The species of deciduous shrub capable of initiating growth the earliest (in this case *Salix*) was able to use a portion of the available N pool otherwise reserved for plant types active early in the growing season, such as forbs, graminoids, mosses and lichens. Therefore, *Salix* became the dominant deciduous shrub in this scenario. *Salix* competed with graminoids for early season available N and with both graminoids and evergreen shrubs for later season available N, thus altering community composition. Total community NPP did not increase as

a result of N acquisition by *Salix*, rather than graminoids, early in the growing season, even though *Salix* has a greater biomass:N ratio than graminoids. This is due to relatively low N availability during the early part of the growing season (compared to later, warmer parts of the growing season) in our model. If changes in the competitive interactions among species with different biomass:N ratios occur during a time of high N availability, we would expect to see substantial changes in NPP. Total biomass did, however, increase with greater variability in timing of growth as the slower-turnover *Salix* replaced the faster-turnover graminoids.

Based on our sensitivity analysis, it appears that aggregation will have the greatest impact when the species or groups being combined include several community dominants that differ with respect to influential attributes in the model. Therefore the effects of aggregation are likely to be greatest when simulating systems with high structural and functional diversity (e.g. tussock tundra or tropical savanna), in other words, systems where it is difficult to effectively partition plant attribute variance among functional types. The degree to which competitive interactions affect the structure

and function of a system is also a key factor in determining an appropriate level of aggregation. It may make sense not to aggregate a group where the competitive balance of components within the group is likely to be altered as a result of environmental change.

One example is that there are strong competitive interactions simulated within the model between deciduous and evergreen shrubs. Deciduous and evergreen shrubs were strongly negatively correlated among model executions ($r = -0.96$), with the greatest correlation ($r > 0.99$) occurring in the sensitivity analysis of the biomass:N parameter. Since these two types of shrubs have some important differences in parameters (e.g. biomass turnover), aggregation into a single shrub component could substantially alter the model results. As a second example, warmer temperatures in ArcVeg would shift the balance within deciduous shrubs toward a domination of *Alnus*, which would also have important implications for the biogeochemical cycling of the system, because of differences in N concentrations (and N-fixing capabilities) between *Alnus* and other deciduous shrubs. In a more aggregated model these effects would be absent.

Aggregation analysis

Our methods of aggregation kept mean parameter values constant (using simple or weighted means) while decreasing the variability of the parameter values. Theoretical modeling exercises conducted by other investigators (Rastetter and Shaver 1995, Smith 1997) have found results consistent with ours, that averaging species parameter values alters the simulated properties of ecosystems. Smith (1997) used plant growth rate along an environmental gradient as the sole parameter of interest in a plant functional type modeling experiment. In an analysis of a single aggregation of five species, he suggested that averaging the plant growth parameter underestimated total biomass compared to the more detailed simulation. Smith's (1997) reasoning was that in the more detailed simulation using five species, the species with the fastest growth rate (and usually greater than average biomass) dominates and determines the total biomass of the system. Our analysis has similar implications, given that the fully aggregated scenario using simple means substantially underestimated total biomass compared to the most detailed simulation (Fig. 5c). The combination of the five plant parameters in ArcVeg that is most favorable for incrementing biomass determines the plant types that come to dominate, thus controlling N uptake and total community biomass in the species-level simulation. When Smith (1997) grouped species into multiple functional types, the results from the aggregate scenarios were similar to those from the species-level simulation. This is again relatively consistent with our results, as the simulations

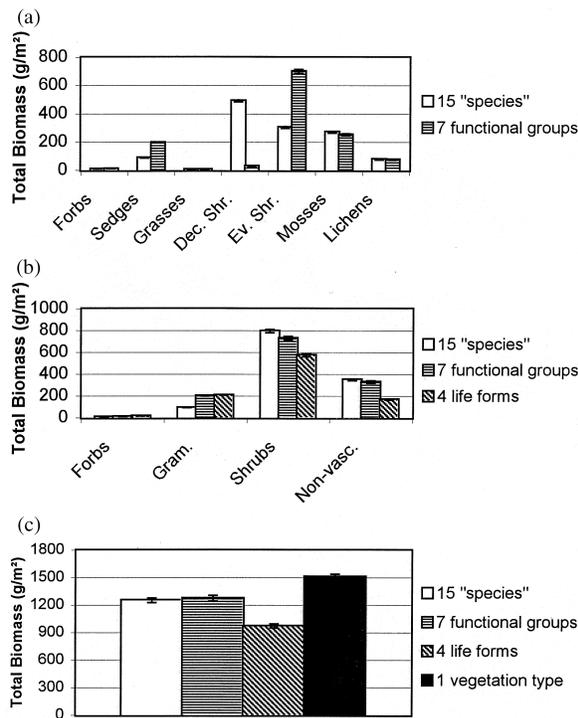
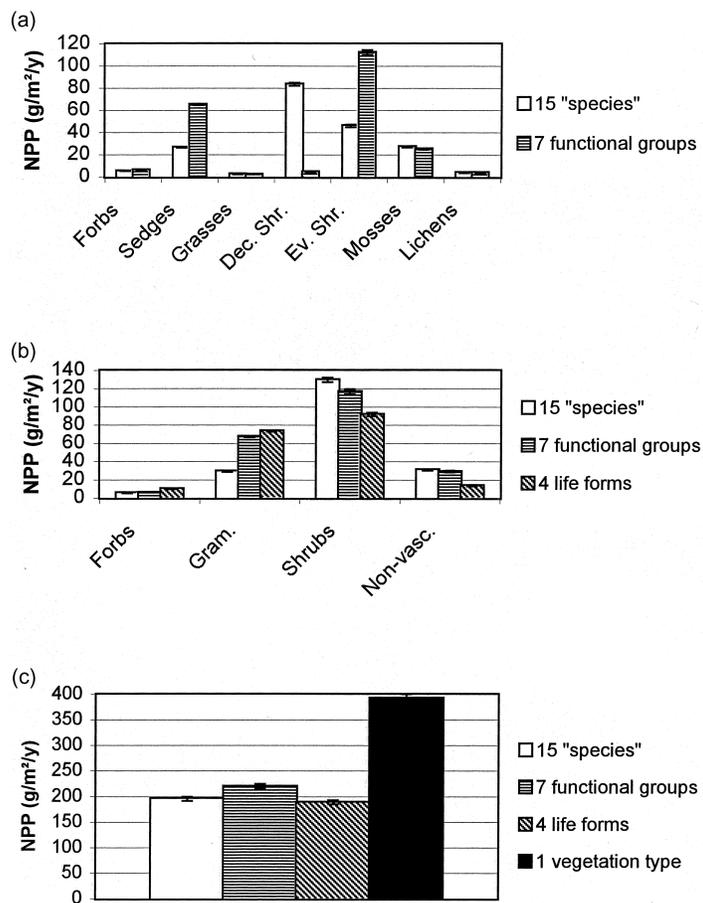


Fig. 7. Total plant biomass (above- plus belowground in g m^{-2}) for a) seven plant functional types at two levels of aggregation, b) four life forms at three levels of aggregation, and c) the entire plant community at four levels of aggregation, using weighted means for averaging parameter values. Data are means \pm standard error, $n = 40$ replicate simulations (data for each replicate simulation are means across 200 yr and 100 patches).

Fig. 8. Net primary production (above- plus belowground in $\text{g m}^{-2} \text{ yr}^{-1}$) for a) seven plant functional types at two levels of aggregation, b) four life forms at three levels of aggregation, and c) the entire plant community at four levels of aggregation, using weighted means for averaging parameter values. Data are means \pm standard error, $n = 40$ replicate simulations (data for each replicate simulation are means across 200 yr and 100 patches).



using seven functional types generated total biomass similar to the species-level analysis.

Methods of aggregation other than averaging have been evaluated (Rastetter et al. 1992, Rastetter and Shaver 1995, Smith 1997). Smith (1997) found that aggregations using the maximum of component parameter values overestimated total biomass compared to detailed simulations; this occurred because, in the species-level analysis, even though the species with the fastest growth rate dominated, it did not exclude the other species from the community. Our analysis using a weighted average of parameter values, based on observed differences in abundance among plant types, also overestimated total community biomass. Rastetter and Shaver (1995) discuss a more complex method of aggregation that adequately represents the dynamics of individual species. However, the methodology requires execution of simulations at both the aggregated and detailed levels before recalculating aggregate parameter values. Additionally, aggregate parameter values need to be calculated for each mix of species expected in a dynamic simulation.

Simulated net primary production in our analysis was greatest in the most aggregated scenarios. This is in contrast to the fact that total biomass was least in the

most aggregated scenario using simple means (Fig. 5c). This occurred because all other scenarios maintained similar values for the annual proportion of biomass senescing (0.15–0.17), whereas the single vegetation type scenario using simple means had proportion senescing of 0.26. The dominance of shrubs and non-vascular plants in the species-level, functional-type and life form simulations, led to the lower turnover rate of biomass in these scenarios (Fig. 5b).

Plant community composition also varied among the different levels of aggregation. Differences in graminoid, shrub and non-vascular plant biomass among the different aggregation levels (Figs 5b, 7b) would likely influence ecosystem processes such as litter decomposition rates, soil heat flux, CO₂ fluxes, water and energy exchange, and runoff (Hobbie 1996, McFadden et al. 1998, Walker et al. 1998, Grogan and Chapin 1999). ArcVeg and most other ecosystem models currently do not simulate many of these feedback mechanisms (see Epstein et al. 1999, Herbert et al. 1999 for exceptions), despite their importance to ecosystem functioning (e.g. Melillo et al. 1982, Pastor et al. 1984, Vitousek et al. 1987, Wedin and Tilman 1990, Epstein et al. 1998). Increasing the complexity of ArcVeg with respect to ecosystem feedbacks would probably alter

the results, depending on the magnitude and direction of the feedbacks between ecosystem structure and function. However, the enhanced realism gained by adding structural complexity to the model must be balanced against the increased probability of modeling artifacts and error propagation.

While increasing input parameter variability in ArcVeg affected the means of total biomass and net primary production, the variance in these properties increased only minimally. In fact, coefficients of variation in total biomass and NPP ranged from 10% to 18% across the different aggregation levels. In all cases, the coefficients of variation for output variables was least for the single vegetation type simulations and greatest for the seven functional type simulations. This may largely be explained by the fact that nitrogen is limiting in the model, and plants in all simulations almost always use the entire available N pool. Essentially, if one plant type in the model is not using available N, another plant type will. The relationship between input variance and output variance might be different if other resources were limiting or if N were not completely conserved.

Regional implications

The North Slope region of Alaska includes approximately 200 000 km² of tundra vegetation, bare soil, water and ice (Muller et al. 1999). The moist acidic, tussock-tundra simulated by ArcVeg is identical to the Moist, Dwarf-Shrub, Tussock-Graminoid Tundra classified by Muller et al. (1999) which encompasses 28% of this region. Aggregating the simulated plant community from 15 species to one vegetation type decreased total plant biomass by 424 g m⁻² using simple means and increased total biomass by 258 g m⁻² using weighted means. Assuming that plant biomass is approximately 45% carbon (Salisbury and Ross 1992), this equates to +191 g C m⁻² and -116 g m⁻², respectively. Extrapolating to 28% of the North Slope suggests either an underestimation of approximately 1.07 × 10¹³ g C or an overestimation of 6.50 × 10¹² g C in plant biomass for moist acidic tundra in the region. This is approximately a 15–25% difference in either direction (McGuire et al. 2000). Using the same method of calculation, aggregation of vegetation could overestimate regional NPP by 1.10 × 10¹³ g C yr⁻¹ (~50% overestimation), again for just moist acidic tundra in Alaska, which is only 14% of the global area of tussock tundra (Bliss and Matveyeva 1992).

Conclusions

Aggregating vegetation in models of plant community and ecosystem dynamics reduces the variability in at-

tributes of plants. This reduction in variability can influence a variety of ecosystem properties including total plant biomass or C, net primary production, and plant community composition. This occurs because variability in plant attributes promotes competitive interactions that lead to the dominance of plants with certain characteristics; these dominant plant types are those that control the properties of the ecosystem. From our results, it appears that aggregating vegetation from its most detailed form (in this case 15 plant types) into seven plant functional types did not substantially alter whole ecosystem properties, such as total biomass and net primary productivity (although it did influence plant community composition). Further aggregation to life forms or vegetation types, however, did affect these whole ecosystem attributes. Changes in ecosystem characteristics as a result of aggregating vegetation in models will depend on 1) the parameter set, 2) how these parameters alter the plant community composition through resource acquisition and competitive interactions, 3) the parameter values of the dominant plant types, 4) how these parameter values alter the properties of the ecosystem, 5) the nature (non-linearity) of the model functions using the aggregated parameters (Rastetter et al. 1992) and finally 6) method of aggregation.

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