

Dynamics of phytoplankton succession coupled to species diversity as a system-level tool for study of *Microcystis* population dynamics in eutrophic lakes

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Abstract

Many of the processes that influence initiation and development of harmful algal blooms (HABs) in lake ecosystems also affect the nature of phytoplankton population overturn—here referred to as the dynamics of succession—and species diversity. Consequently, the dynamics of succession and species diversity might reflect the lake's resistance to HABs. We explored this idea by developing a potential system-level tool based on the coupling of these two characters, where the dynamics of succession were quantified using a first derivative index, and tested it in a single lake plagued by recurrent blooms of *Microcystis aeruginosa*. Our analysis showed that if nonbloom periods were characteristic of either low succession dynamics or low species diversity, *M. aeruginosa* blooms followed. However, when succession dynamics and species diversity were both high for an extended period, a *M. aeruginosa* bloom did not follow. Should this relationship hold true in other lakes and when blooms are not as severe, a coupling of succession dynamics to species diversity might prove useful as a tool to evaluate *M. aeruginosa* population dynamics at the system level. Data at the species level were needed to elucidate this inverse relationship between *M. aeruginosa* bloom initiation and the dynamics of succession coupled to species diversity. When species data were grouped into coarse taxonomic categories (i.e., groups discernable using *in vivo* absorption spectra) the relationship was not detectable.

Causative organisms of harmful algal blooms (HABs) in lake ecosystems are diverse and include representatives from the cyanobacteria, chrysophyte, and dinoflagellate taxonomic groups (Zohary et al. 1996; Berman et al. 1998; Lindholm et al. 1999). Bloom-initiating mechanisms are also diverse and include the onset of water column stratification, shifting nutrient ratios, and increased hydraulic residence time (Paerl 1988; Zohary et al. 1996; Sellner 1997; Roelke et al. 1999a; Roelke and Buyukates 2001). Most likely, processes leading to bloom initiation do not act singularly. A more likely scenario is that several processes act synergistically. Consequently, the study of HAB population dynamics as they relate to environmental forcing factors in lake ecosystems will require diagnostic tools operating at the system level.

In this study, we develop a system-level tool that is based on two ecological concepts: the diversity–stability hypothesis and the nature of a phytoplankton population overturn. For the purposes of this manuscript, the nature of a phytoplankton population overturn is characterized by the rate of population accumulation, the magnitude of accumulated biomass, and the rate of population decrease. We refer to this as the dynamics of succession, where high dynamics signifies rapid accumulation and decrease of phytoplankton populations that, prior to replacement, attain high biomass con-

centrations. In this paper, we also assume that HABs in lake ecosystems represent a deviation from the “normal” biological and ecological systems, especially in lakes where recurrent and near-monospecific HABs have disrupted the normal pattern of phytoplankton succession.

Theoretical basis—There is growing evidence that ecosystems characteristic of multitrophic interactions show a positive correlation between species diversity and ecosystem stability, where the controlling mechanism is functional redundancy within trophic levels (Borrvall et al. 2000; Loreau 2000; Aoki and Mizushima 2001). Like many aquatic systems, lakes are characteristic of multitrophic interactions. For example, phytoplankton communities interact with virus, fungi, bacteria, zooplankton, and higher trophic levels (Sommer 1989a). Phytoplankton species diversity in lake ecosystems is influenced by many biotic and abiotic processes that include the magnitude and frequency of inflow events with associated nutrient loading, infection by species-specific pathogens, and selective grazing (Donk 1989; Sterner 1989; Romo and Miracle 1995; Holfield 1998; Figueredo and Gianni 2001). Some of these processes are also linked to HAB initiation. For example, a combination of drought years and high nutrient loading most likely allowed for the recurrent blooms of *M. aeruginosa* and concurrent low phytoplankton species diversity in Hartbeespoort Dam (Zohary et al. 1996). It stands to reason that in some lake ecosystems, at certain times, phytoplankton species diversity will correlate to lake ecosystem stability, where stability refers to the lake's resistance to HABs.

The dynamics of phytoplankton succession are a function of many of the same environmental processes that affect species diversity. For example, the onset of spring bloom in dimictic lakes is controlled by the relief of light limitation at a time when nutrient concentrations are high and grazer abundance is low. This results in rapid growth and high ac-

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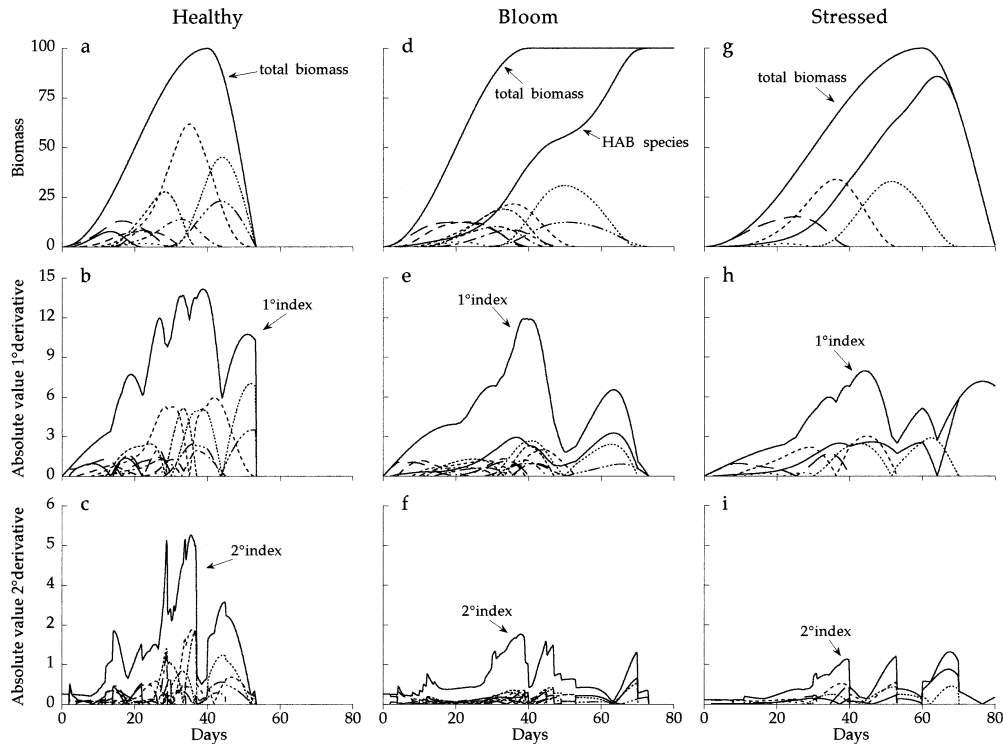


Fig. 1. Hypothetical phytoplankton succession patterns and dynamics in response to a favorable disturbance in a healthy (a–c), bloom-affected (d–f), and stressed (g–i) phytoplankton community. The healthy community shows a sequence of population peaks representing a continuum of species with decreasing competitive ability, but increasing resistance to grazing losses (but not to the point of being inedible), and an eventual grazing removal of all species (a). Succession dynamics, as indicated by the first and second derivative indices (b, c), are highest for the healthy scenario. Succession dynamics are more sluggish in the bloom-affected (d) and stressed (g) scenarios. Although not so obvious when comparing the graphs showing biomass changes (a, d, g), it is very clear when comparing the first (b, e, h) and second (c, f, i) derivative indices.

accumulated biomass (i.e., high dynamics of r-selected phytoplankton populations, where succession is influenced by the limitation of various nutrients, infection by species-specific pathogens, and selective grazing) (Sommer et al. 1986; Sommer 1989b; Horne and Goldman 1994). Similarly, during summer months, phytoplankton succession occurs among k-selected populations, in part, as a function of nutrient recycling and infection by species-specific pathogens (Horne and Goldman 1994).

The dynamics of succession, as with species diversity, might be reflective of ecosystem stability, where again stability refers to the lake's resistance to HABs. Although this concept has not been demonstrated in the natural environment, it can be visualized by referring to a conceptual model depicting a phytoplankton community comprised of many edible phytoplankton forms that differ in their ability to compete for nutrients and their vulnerability to grazing processes (Sommer 1989b; Sterner 1989; Sterner and Hessen 1994). Following a favorable disturbance (e.g., a large nutrient pulse at a time of nutrient limitation), a succession pattern can be envisioned as depicted in Fig. 1a, where the phytoplankton species that first respond to the nutrient addition are the most pronounced r-selected competitors and are the most susceptible to grazing losses (Riegman 1991; Horne

and Goldman 1994; Sterner and Hessen 1994). Subsequent population peaks represent a continuum of species with decreasing competitive ability, but increasing resistance to grazing losses (but not to the point of being inedible). Eventually, all phytoplankton forms give way to a clear-water phase because of heavy grazing pressure (Sommer et al. 1986).

The dynamics of succession, in this case, can be quantified by analyzing the sum of the absolute value of the first and second derivatives of the population curves for each competing species (explanation of this approach is provided in the Methods section). Values for these derivative indices are highest when community succession is the most dynamic (i.e., individual populations are growing rapidly and to high biomass concentrations and are rapidly being grazed) (Fig. 1b,c). Because this scheme adopts a summation of all competing populations, species richness is also an important factor affecting the values of the derivative indices.

A possible effect of HAB formation on the dynamics of phytoplankton succession can be illustrated using the same hypothetical phytoplankton community, but with the substitution of one species with a slower growing and grazing-resistant species. In this scenario, the only loss factor to the grazing-resistant species is flushing, and the only process

limiting its growth rate is competition for limiting nutrients (competitors are affected by flushing, competition, and grazing). Because the grazing-resistant species continues to slowly accumulate biomass, other competing species will not grow to biomass concentrations as high, or as fast, as in the first scenario. This happens because the grazing-resistant species will continue to sequester greater amounts of growth-limiting nutrient (Roelke and Buyukates 2000) and because the selective grazing pressure on competing phytoplankton increases with the increase in the biomass of the grazing-resistant species (Sterner 1989). This trend can be discerned, but only moderately, by comparing the hypothetical population curves of the second scenario with that of the first (Fig. 1a,d). The trend can easily be seen, however, by comparing the derivative indices of the second scenario with those of the first (Fig. 1b,c,e,f), where the derivative peaks are larger and occur over longer periods (i.e., succession in the first scenario is more dynamic).

This derivative scheme might show similar trends when grazing-resistant HAB species are not yet present; that is, the lake ecosystem is vulnerable but not yet affected by the HAB species. For example, ecosystems where the timing of various forcing functions are out of sync with the timing of ecological processes affecting phytoplankton community dynamics (i.e., frequency of disturbances are too low or too high, Connell 1978), might be characteristic of low species richness and low succession dynamics. Similarly, ecosystems affected by various stressors (e.g., pollution of heavy metals, hydrocarbons, organic carbon, etc.) might also be characteristic of low species richness and low succession dynamics. As a result, the system might be more sensitive to take-over by previously less prevalent species or subject to invasion by exotic species. Again, low succession dynamics and low species richness (Fig. 1g) result in low first and second derivative indices (Fig. 1h,i).

Objectives—Because phytoplankton species diversity and the dynamics of succession are both influenced by many biotic and abiotic processes (some of which influence HAB initiation in lakes) and might both be linked to ecosystem stability (e.g., a lake's resistance to HABs), they are explored here as a potential system-level tool tailored to the study of HAB population dynamics. In this manuscript, we test the potential system-level tool using a detailed phytoplankton record spanning 5 yr that documents recurrent blooms of *M. aeruginosa* in a hypertrophic lake, Hartbeespoort Dam, South Africa (Zohary et al. 1996; Hambright and Zohary 2000). Our findings are specific to this lake and might not be applicable to other HAB-forming species or other lake ecosystems. The system-level tool is first tested at the species level. We then perform a sensitivity analysis by grouping the phytoplankton species into categories that are discernable using current optical technology.

Methods

The previously reported data set on which we relied documented population shifts in 23 of the 73 observed species in Hartbeespoort Dam (Hambright and Zohary 2000). Numerical values corresponding to population dynamics graphs

were obtained by digitizing the published figure and using a shareware graph-to-data application. Zohary et al. (1996) reported that of the 73 species observed, only 20 were occasionally abundant, and only 5 ever became dominant. Hence, the digitized data set captures the prevalent succession patterns that occurred in Hartbeespoort Dam.

Initially, the scanned data was at greater resolution than the original data, which was based on weekly and biweekly sampling. To adjust for this difference, the scanned data was interpolated to a vector containing one element every 7 d, where the scanned data points were averaged over a 7-d period. This resulted in an evenly spaced and monotonic data set that lent itself to determination of the first derivative using a common three-point equivalent formula.

$$f'(x_0)_i = \frac{1}{2h}[f(x_0 + h)_i - f(x_0 - h)_i] - \frac{h^2}{6}f^{(3)}(\xi_1) \quad (1)$$

For each species, $i = 1-23$; $f'(x_0)_i$ was the species-specific value of the first derivative of the population curve at a specific time, h was the 7-d time step, $f(x_0 + h)_i$ and $f(x_0 - h)_i$ were the species-specific biomass values of the population curve 7 d after and 7 d prior to a specific time, respectively, and $(h^2/6)f^{(3)}(\xi_1)$ was an error approximation (Burden and Faires 1985).

Because this potential system-level tool is based on the assumption that the degree of succession dynamics is important, the rate of increase and the rate of decrease in a population were treated equally. Consequently, the absolute value of the first derivative was used for each population curve. In addition, this potential indicator assumes that species richness is important; thus, all derivative functions of population curves were summed. Therefore, the formula used to determine the first derivative index was as follows.

$$1^\circ \text{ Index} = \sum_{i=1}^{23} |f'(x_0)_i| \quad (2)$$

For species i at a specific time, $|f'(x_0)_i|$ was the absolute value of the first derivative.

Applying first and second derivative indices to hypothetical phytoplankton community shifts (Fig. 1) indicated that the second derivative index, which was generated in the same way as the first derivative index, was more sensitive to succession dynamics than the first derivative index. In this context, the second derivative represented the acceleration or deceleration of population growth or reduction. The second derivative index, however, required more closely spaced data in order to generate smooth curves. Because the scanned Hartbeespoort Dam data were averaged to 7-d resolution, the second derivative index was not calculated. We mention this point, however, because new technologies capable of delineating phytoplankton to the taxonomic level of genus over very short time intervals (discussed later) will allow the application of the second derivative index.

This potential system-level tool also assumes that species diversity is an important indicator of ecosystem stability. Species diversity was determined using the Shannon–Weaver index.

$$H' = \sum_{i=1}^{23} p_i \log_2(p_i) \quad (3)$$

The proportion of biomass of species i relative to the total biomass at a specific time was p_i .

In an attempt to discern temporal differences in population succession dynamics and species diversity, arbitrary levels were selected for both the first derivative index and the Shannon–Weaver species diversity index. In this case, the level was 2 for each of the indices, where the first derivative index or diversity index was considered high if the value was above the selected level or low if the value was below the selected level. The phytoplankton population data could then be divided into four categories, in which the first derivative index and species diversity were either both high (High–High) or both low (Low–Low), the first derivative index was high but diversity low (High–Low), or the first derivative index was low and the diversity high (Low–High). This categorization of the population data was then used to investigate whether there was a trend between the dynamics of phytoplankton succession coupled with species diversity to the occurrence of *M. aeruginosa* blooms.

To reinforce trends observed in the indices and the four categories (High–High, Low–Low, High–Low, Low–High) discriminant analysis of the 260 time points (weekly intervals over 5 yr) were performed using commercial software (SPSS). Discriminant analysis is a statistical technique that uses linear combinations of independent variables to form a basis for a classification scheme. For our application, the independent variables were the 23 phytoplankton populations. We opted for a standard discrimination method, in which all independent variables were entered simultaneously into the analysis. By using a standard method, group coefficients for function 1 were not as great as the stepwise method, but group coefficients for function 2 were greater, which in this case resulted in better overall discrimination between the four categories. Three discriminant analyses were conducted. The first used only the population biomass data, the second used only the first derivative index data, and the third used both the population and first derivative index data.

This potential system-level tool, specific to *M. aeruginosa* bloom development in this study, requires data of fine-scale temporal resolution. But it might not require taxonomic resolution at the species level; that is, the summed rate of biomass change of all “lumped” groups comprising similar phytoplankton members might show the same trend as the summed rate of change of all populations. Therefore, we tested the practicality of this potential tool by conducting a sensitivity analysis in which the phytoplankton species were grouped into categories discernable using current optical technologies.

Current technologies in the arena of in situ optics are beginning to support the measurement of hyperspectral absorption and scatter properties (Roelke et al. 1998; Weidemann et al. 1998). Because these instruments can be deployed for long periods, high-resolution temporal data necessary for this system-level tool can be obtained, including the more sensitive second derivative index. Taxonomic

resolution of the data, however, will be coarse. For example, using discriminant analysis on hyperspectral absorption data gathered from many individual phytoplankton cultures, it was demonstrated that five general taxonomic groups could be delineated: cyanobacteria, dinoflagellates, green algae, diatoms, and other Chrysophytes (Roelke et al. 1999b). Therefore, we grouped the scanned Hartbeespoort Dam data into general taxonomic groups, which were cyanobacteria, general flagellates, green algae, and diatoms. This grouping assumed that flagellates generally were discernable from non-flagellated algae. In addition, an “other Chrysophytes” group was not formed because Chrysophytes other than diatoms were not represented in the 23 reported species from Hartbeespoort Dam.

The first derivative index and the diversity index were then calculated using Eqs. 1–3, but in this case, $i = 1$ –4 and represented the four general taxonomic groups. As before, to better enable us to discern temporal differences in coarse taxonomic succession dynamics and taxonomic diversity, arbitrary values for the first derivative index and taxon diversity index were selected that enabled us to categorize the data into four groups (High–High, Low–Low, High–Low, Low–High).

Results

The timing of the recurrent blooms of *M. aeruginosa*, as reported by Hambright and Zohary (2000) in their phytoplankton biomass data, was easily discerned by looking at the absolute value of the first derivative data. During the winter and spring seasons in each of the 5 yr, *M. aeruginosa* dominated the first derivative index, and in the first 4 yr *M. aeruginosa* dominated in the late fall and early winter months (Figs. 2–6). The timing of other blooms (nontoxic), where a single species dominated the phytoplankton, also is seen easily (e.g., blooms of the green algae *Oocystis lacustris* [Figs. 2–5] and *Cartia cordiformis* [Fig. 5]), as well as a period when there was co-occurrence of the diatom *Cyclotella meneghiniana* during a *M. aeruginosa* bloom (Fig. 2). Similarly, periods when many species co-occurred without dominance of any one species can be discerned.

When considering only the first derivative index, there was no trend between periods of high phytoplankton succession dynamics and whether *M. aeruginosa* blooms ensued. Neither was there a trend with the species diversity index (Fig. 7). However, when both the first derivative index and the species diversity index were considered together, a trend with *M. aeruginosa* bloom occurrence was apparent. For example, on five occasions, there were periods when both phytoplankton succession dynamics and species diversity were high (i.e., the High–High category; see the comparison bar, Fig. 7). However, only during the fifth year, when no subsequent *M. aeruginosa* blooms were documented, did a prolonged High–High period occur (two consecutive 3-week periods of High–High, separated by a week). In the first 4 yr of the record, prolonged conditions categorized as Low–Low, High–Low, and Low–High all occurred prior to *M. aeruginosa* bloom development (see the comparison bar, Fig. 7).

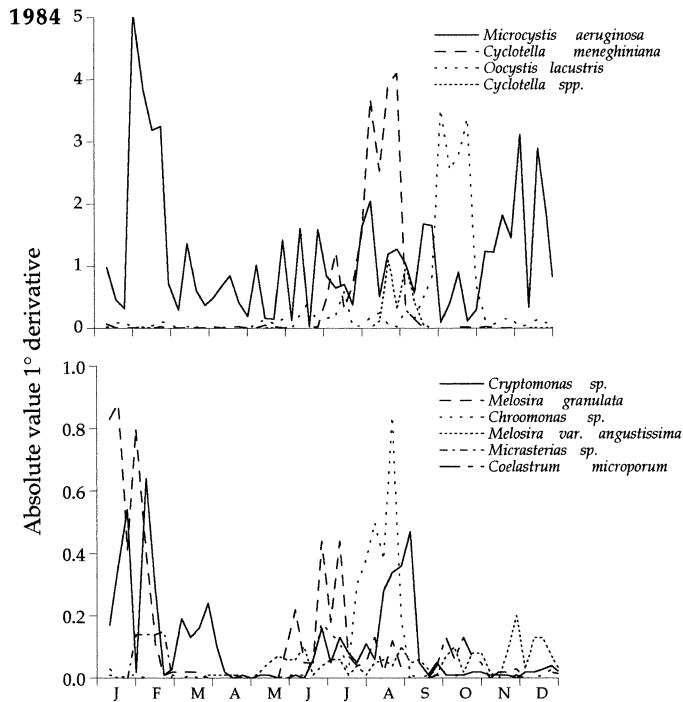


Fig. 2. First derivative index values for phytoplankton population data at the species level from Hartbeespoort Dam, South Africa, in 1984, with species showing higher dynamics depicted in the upper graph. The *M. aeruginosa* bloom dominated the dynamics of the phytoplankton community from the winter through spring months, a reoccurring pattern in this data, whereas separate blooms of *Cyclotella* sp. dominated the dynamics of the phytoplankton community in summer and fall months.

These observations were reinforced using the discriminant analysis, in which our division of the population and first derivative index data into four categories produced distinctive groupings. Both population and first derivative index data, however, were required to achieve good discrimination. For example, discriminant analysis using only the population data (Fig. 8a) showed a weak separation of the four categories (i.e., only 74.4% of “grouped” cases were correctly classified, Table 1). A discriminant analysis using only the first derivative index data (Fig. 8b) showed much stronger delineation of the four categories (i.e., 93.4% of grouped cases were correctly classified), but the High–High category was incorrectly classified as one of the other categories in 44.4% of the High–High cases (Table 1). The best delineation between the four categories occurred when both population and first derivative index data were used in the discriminant analysis (Fig. 8c). In this case, 94.6% of grouped cases were correctly classified, the High–High category was incorrectly classified as one of the other categories in 22.2% of the cases, and only one of the other categories was incorrectly classified as the High–High category in 2.2% of the cases. In all cases where the High–High category was incorrectly classified, a *M. aeruginosa* bloom followed. All High–High cases that were not followed by a *M. aeruginosa* bloom were correctly classified in the High–High category.

When using the grouped data (i.e., coarse taxonomic resolution), prolonged periods categorized as High–High oc-

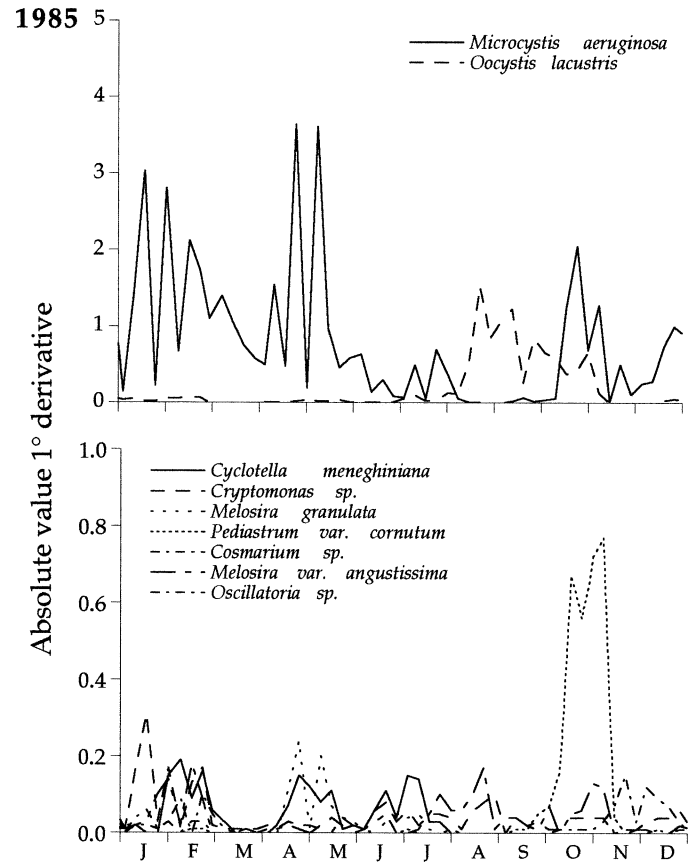


Fig. 3. First derivative index values for phytoplankton population data at the species level from Hartbeespoort Dam, South Africa, in 1985. The *M. aeruginosa* bloom dominated the dynamics of the phytoplankton community through most of the year, except in August and September, when an *O. lacustris* bloom dominated.

curred through out the 5-yr period (see the comparison bar, Fig. 9). In other words, when the population data and the first derivative index data were grouped into categories discernable using current in situ optical technology, it was not possible to make out any temporal differences between the dynamic nature of succession events and taxonomic diversity to occurrences of *M. aeruginosa* blooms (Fig. 9).

Discussion

Our evaluation of this potential system-level tool for the study of HAB population dynamics and ecosystem stability in lakes is specific to recurrent blooms of *M. aeruginosa* in Hartbeespoort Dam. These same trends must be observed in other lakes and with other HAB-forming species before our evaluation is complete. In addition, our findings were dependent on the selection of the threshold values for each index. For the population data, we arbitrarily chose a value of 2 for the first derivative index and the species diversity index. Different threshold values were used with the grouped data (coarse taxonomic resolution) in an attempt to produce useful results. Should this tool prove useful after further testing and technology development (discussed below), it is likely that threshold values will vary between systems tar-

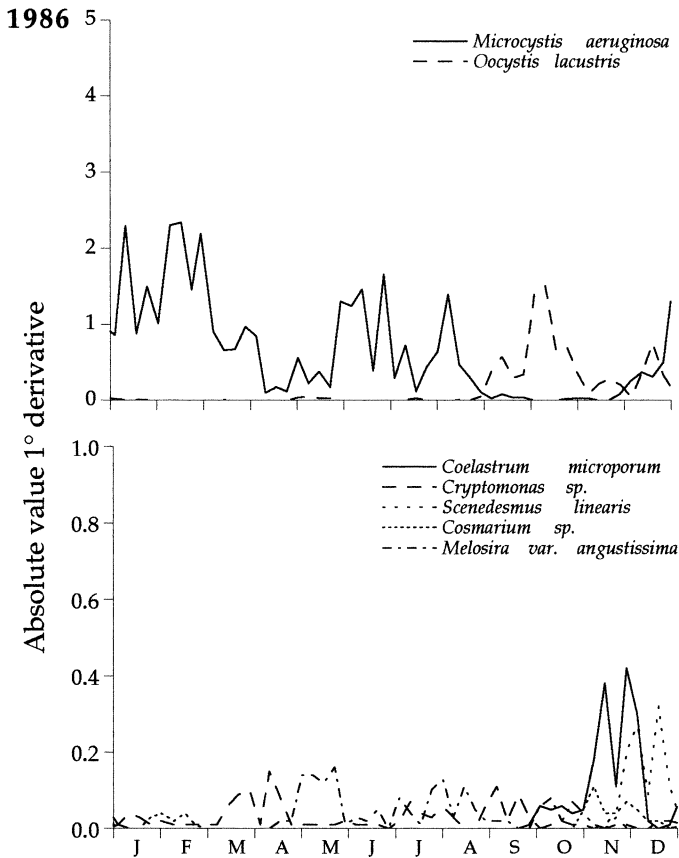


Fig. 4. First derivative index values for phytoplankton population data at the species level from Hartbeespoort Dam, South Africa, in 1986. The trend is very similar to that observed in the previous year, when the *M. aeruginosa* bloom dominated the dynamics of the phytoplankton community through most of the year, except in August and September, when an *O. lacustris* bloom dominated.

geted for study and will be based on a previous knowledge of phytoplankton community composition and dynamics.

Population and first derivative data at the species level—As demonstrated using the first derivative index and Shannon–Weaver species diversity index and as reinforced using discriminant analysis, there is an inverse relationship between the dynamics of phytoplankton succession coupled to species diversity during nonbloom periods to the eventual formation of *M. aeruginosa* blooms in Hartbeespoort Dam. In other words, in Hartbeespoort Dam this proposed tool did provide a measure of the lake’s stability (i.e., its resistance to *M. aeruginosa* blooms). Interestingly, using only discrimination between the four categories of population abundance data was not nearly as defined as discrimination based only on succession dynamics. In the case of Hartbeespoort Dam, phytoplankton community structure, as measured by the Shannon–Weaver index, was not as useful as the community dynamics when evaluating the lake’s vulnerability to *M. aeruginosa* blooms. A coupling of community structure and dynamics, however, produced the most useful system-level tool. Potential mechanisms explaining the occurrence of each of the four succession dynamics and species diversity cate-

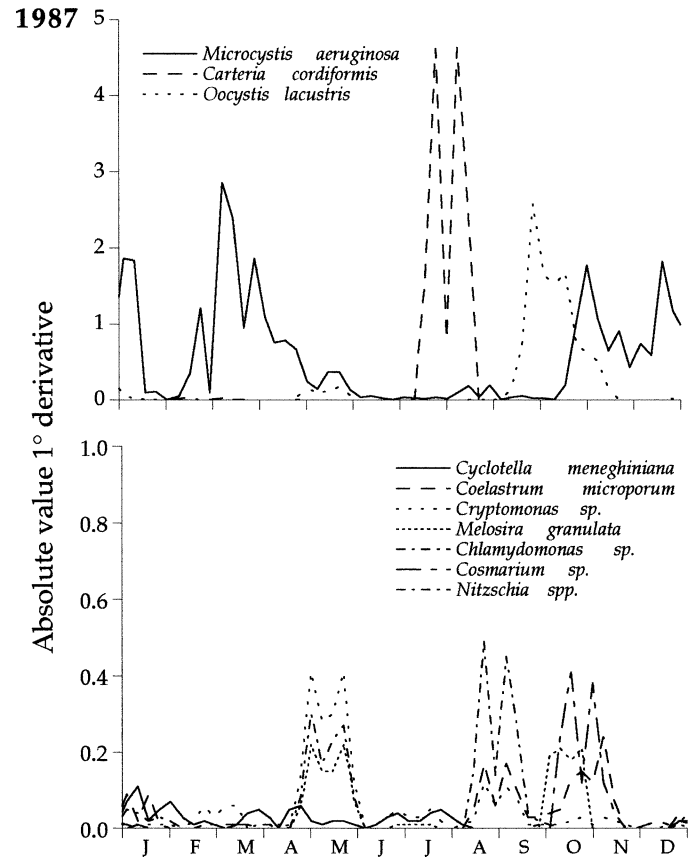


Fig. 5. First derivative index values for phytoplankton population data at the species level from Hartbeespoort Dam, South Africa, in 1987. The *M. aeruginosa* bloom dominated the dynamics of the phytoplankton community from the winter through spring months, which gave way to high dynamics of a summer bloom of *C. cordiformis*. In turn, the dynamics of this bloom gave way to the high dynamics of a *O. lacustris* bloom in the fall, which gave way to another bloom of *M. aeruginosa*, the last documented in this data record.

gories in relation to *M. aeruginosa* blooms fit well with the conceptual model described previously and are discussed below.

Potential underlying mechanisms that might explain prolonged High–High conditions that were not followed by a *M. aeruginosa* bloom were highlighted earlier when discussing the conceptual model (i.e., rapid succession of many fast-growing, relatively edible phytoplankton species following a favorable disturbance). In the case of the Hartbeespoort Dam phytoplankton community, Hambright and Zohary (2000) reported that the disturbance was cessation of a drought period, which resulted in increased flushing of the lake and reduced phosphorus loading. Greater succession dynamics were calculated with the first derivative index because of the large population peaks of *Cryptomonas* sp., *C. meneghiniana*, *O. lacustris*, *Coelastrum microporum*, and *Scenedesmus linearis*, as reported by Hambright and Zohary (2000). Although all of these species were present earlier in the data record, they never occurred synchronously or sequentially as they did in the fifth year. Furthermore, *Cryptomonas* sp., *C. microporum*, and *S. linearis* showed popu-

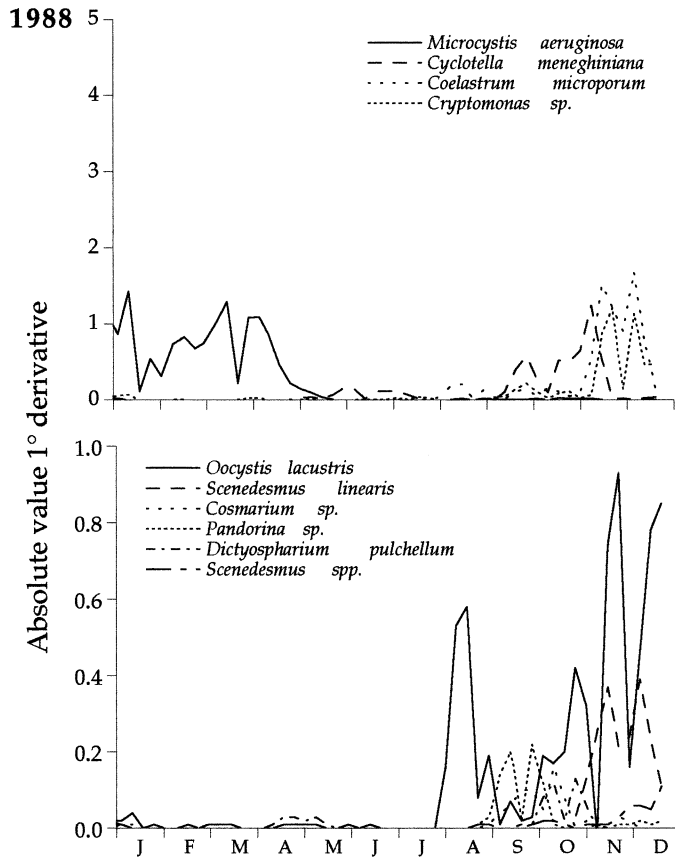


Fig. 6. First derivative index values for phytoplankton population data at the species level from Hartbeespoort Dam, South Africa, in 1988. The *M. aeruginosa* bloom dominated the dynamics of the phytoplankton community in the winter months only. No single species dominated the dynamics of the phytoplankton after this bloom dissipated, and no *M. aeruginosa* bloom returned in the winter of 1989.

lation growth with at least twofold greater maxima over periods similar to previous years. Both of these factors contributed to the high first derivative index value. Greater species diversity resulted because of the concurrent appearance of these species and the appearance of two additional species, *Pandorina* sp. and *Dictyosphaerium pulchellum*, that were only documented in the fifth year of the data record reported by Hambright and Zohary (2000). Of these species, *Cryptomonas* sp., *C. meneghiniana*, and *S. linearis* can be categorized as r-selected, with attributes of fast growth and relative edibility (Sommer 1983; Zohary et al. 1996; Roelke et al. 1997). *C. microporum*, *D. pulchellum*, and *Pandorina* sp. are also relatively fast-growing species, but their edibility is questionable based on their larger size (Dauta 1982; Sommer 1983).

Potential underlying mechanisms that would explain the prolonged Low–Low conditions that occurred during periods between *M. aeruginosa* blooms were also mentioned earlier when discussing the conceptual model; that is, the presence of a grazing-resistant species results in greater preferential grazing on more edible forms, which would result in decreased succession dynamics and species diversity. As reported by Hambright and Zohary (2000), co-occurring species with *M. aeruginosa* during nonbloom periods included *C. meneghiniana*, *Chroomonas* sp., *Cyclotella* spp., and *O. lacustris*. Along with *M. aeruginosa*, *Chroomonas* sp. and *O. lacustris* have been characterized as resistant to grazing and relatively slower to grow (Sommer 1983; Reynolds 1989; Zohary et al. 1996). Increased preferential grazing on the two species of *Cyclotella*, presumably r-selected species, might have decreased their population dynamics. Another possible mechanism that might induce Low–Low conditions during nonbloom periods when *M. aeruginosa* is present is the production of allelopathic chemicals. Such compounds have been shown to suppress the growth of competing phytoplankton, thereby increasing the fitness of the species producing the chemical. This has been documented for some

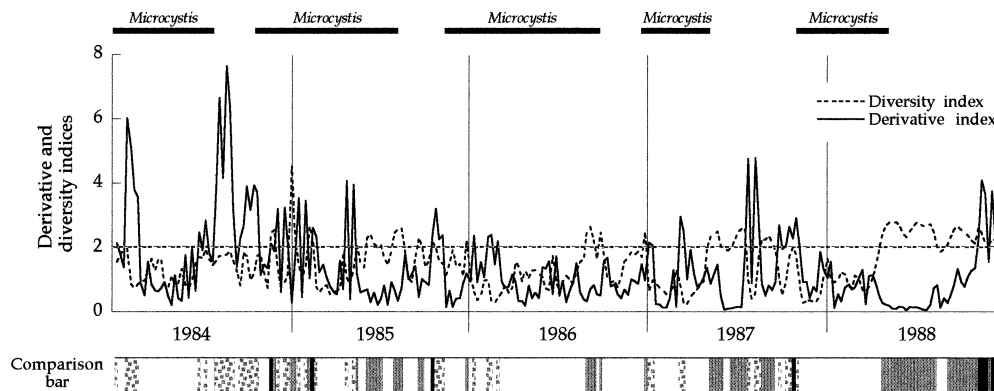


Fig. 7. First derivative index values, based on species-specific population data, and species diversity index values for the 5-yr period. During nonbloom periods, the first derivative index and the species diversity index were either both higher than the threshold value of 2 (indicated with solid fill in the comparison bar); both lower than the threshold (unfilled sections of the comparison bar); higher and lower, respectively (mottled sections of the comparison bar); or lower and higher, respectively (gray sections of the comparison bar). Prolonged conditions of high succession dynamics and high species diversity only occurred in the fifth year, and no *Microcystis aeruginosa* bloom followed.

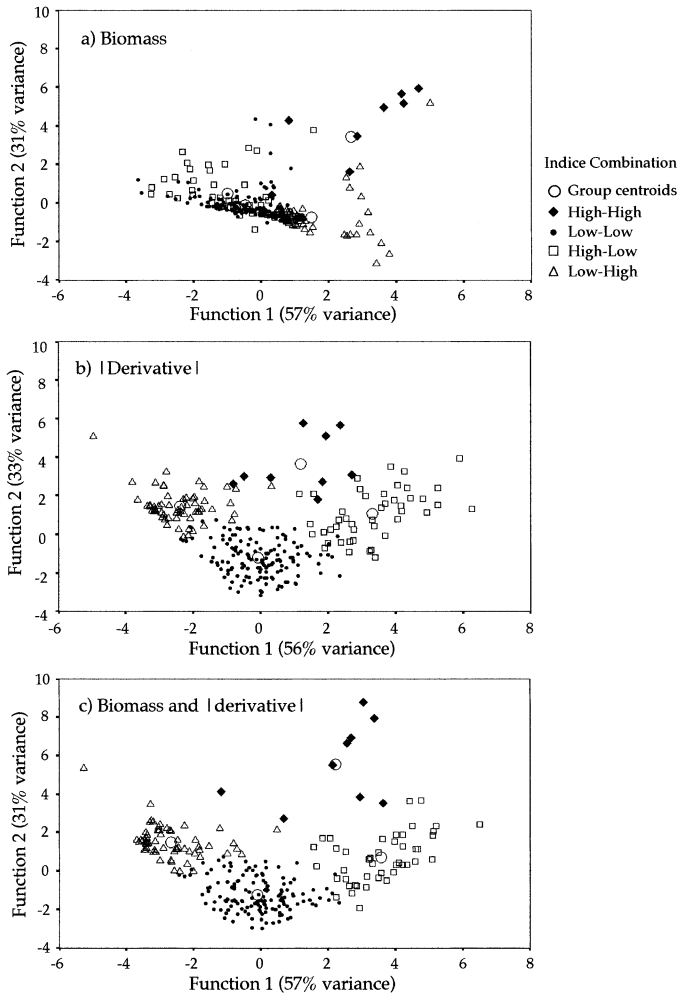


Fig. 8. Discriminant analyses using only the population data (a), only the derivative data (b), and both the population and derivative data (c). Discrimination using only population abundance data between the four categories was not nearly as defined as discrimination based only on succession dynamics, suggesting that knowledge of phytoplankton community structure (population data) might not be as useful as knowledge of community dynamics (derivative data) when evaluating ecosystem stability. A coupling of community structure and dynamics, however, yielded the best discrimination results.

cyanobacteria species (Smith and Doan 1999) and might have been the case for *M. aeruginosa* in Hartbeespoort Dam.

Low–Low conditions in Hartbeespoort Dam also occurred in the absence of *M. aeruginosa*. During these periods, Hambright and Zohary (2000) reported that the phytoplankton community was comprised of *Melosira* var. *angustissima*, *Pediastrum* var. *cornutum*, and *C. microporum*. Although *C. microporum* is a fast-growing species (Dauta 1982), species of *Melosira* and *Pediastrum* are not fast growing and might be less edible based on their large size (Dauta 1982; Horne and Goldman 1994). This might have resulted in greater preferential grazing pressure on *C. microporum*, thereby causing low population dynamics.

Prolonged High–Low conditions also occurred prior to *M. aeruginosa* blooms in the Hartbeespoort Dam data, illus-

Table 1. Number (%) of accurate classifications in the four phytoplankton community groups (succession–diversity) using discriminant analyses of population biomass data only, population dynamics only, and both population biomass and succession dynamics.

Group	No. of cases	Predicted group membership			
		Low–High	High–Low	Low–Low	High–High
Population biomass (74.42% of grouped cases correctly classified)					
Low–High	61	56 (91.8)	0 (0)	3 (4.9)	2 (3.3)
High–Low	45	2 (4.4)	21 (46.7)	21 (46.7)	1 (2.2)
Low–Low	143	17 (11.9)	15 (10.5)	108 (75.5)	3 (2.1)
High–High	9	1 (11.1)	1 (11.1)	0 (0)	7 (77.8)
Population derivative (93.41% of grouped cases correctly classified)					
Low–High	61	60 (98.4)	0 (0)	0 (0)	1 (1.6)
High–Low	45	0 (0)	43 (95.6)	2 (4.4)	0 (0)
Low–Low	143	9 (6.3)	1 (0.7)	133 (93.0)	0 (0)
High–High	9	1 (11.1)	3 (33.3)	0 (0)	5 (55.6)
Population biomass and derivative (94.57% of grouped cases correctly classified)					
Low–High	61	60 (98.4)	0 (0)	1 (1.6)	0 (0)
High–Low	45	0 (0)	43 (95.6)	1 (2.2)	1 (2.2)
Low–Low	143	8 (5.6)	1 (0.7)	134 (93.7)	0 (0)
High–High	9	0 (0)	2 (22.2)	0 (0)	7 (77.8)

trating that high succession dynamics alone did not reflect the vulnerability of this lake to *M. aeruginosa* blooms. Low species diversity might have resulted in a lack of phytoplankton competitors, a lack of alternative food sources for grazers, or both. Both scenarios are conducive to initiation of some HABs (Roelke 2000; Roelke and Buyukates 2001) and might have been the case for the *M. aeruginosa* blooms. High succession dynamics and low species diversity can result in phytoplankton blooms that are not harmful precede HABs. For example, a marine bloom of *Chrysochromulina polylepis* in Scandinavian waters could have been stimulated, in part, by preconditioning of an earlier *Skeletonema costatum* bloom that might have elevated the cobalt and vitamin B₁₂ concentrations (Graneli and Risinger 1995). Similarly, it is postulated that blooms of the marine cyanobacterium *Trichodesmium* sp. could have conditioned waters off the Florida west coast for toxic blooms of *Karenia brevis* by increasing nitrogen availability through N₂ fixation (Walsh et al. 2001). Hambright and Zohary (2000) reported that *M. aeruginosa* blooms in Hartbeespoort Dam were preceded by relatively high populations of *O. lacustris*, resulting in High–Low conditions, which might have stimulated the *M. aeruginosa* blooms in some way. In addition, *C. cordiformis* and *C. microporum* were reported to precede and co-occur, respectively, with *M. aeruginosa*—again High–Low conditions—hinting that these species might also have stimulated *M. aeruginosa* blooms in some way.

Brief and periodic Low–High conditions occurred prior to *M. aeruginosa* blooms, and they occurred extensively in the fifth year when there was no documented *M. aeruginosa* bloom. A plausible mechanism for those years when *M. aeruginosa* blooms did follow the Low–High conditions could be the production of allelopathic compounds, as mentioned before. Another explanation might be that the species

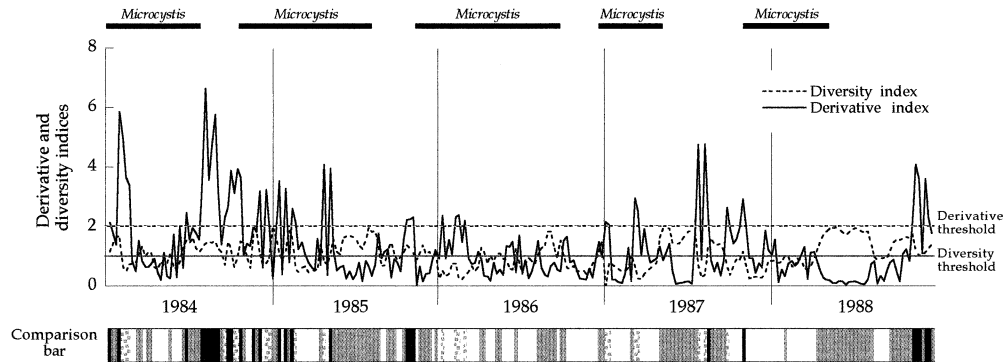


Fig. 9. First derivative index and diversity index values based on taxonomically grouped population data for the 5-yr period. During nonbloom periods, the first derivative index and the taxonomic diversity index were again either both higher than the designated threshold (indicated with solid fill in the comparison bar); both lower (unfilled sections of the comparison bar); higher and lower, respectively (mottled sections of the comparison bar); or lower and higher, respectively (gray sections of the comparison bar). Unfortunately, prolonged conditions of high succession dynamics and high species diversity occurred prior to cyanobacteria blooms.

present were predominately k-selected (i.e., slower growing and more grazing resistant). In other words, niche partitioning might have occurred, resulting in relatively high species diversity but low succession dynamics (Sommer 1989b). This condition might have left the lake vulnerable to *M. aeruginosa* blooms; that is, when conditions favorable to *M. aeruginosa* growth arose, the slower growing k-selected species might not have competed well. Hambright and Zohary (2000) reported that *Melosira granulata*, *M. var. angustissima*, *Chroomonas* sp., *Oscillatoria* sp., *P. cornutum*, *Nitzschia* spp., and *Chlamydomonas* sp. all appeared during Low–High conditions that were followed by a *M. aeruginosa* bloom. They did not occur during the Low–High conditions in the fifth year, when there was no subsequent *M. aeruginosa* bloom. With the exception of *Chlamydomonas* sp., many of these species can be characterized as k-selected; that is, they are relatively slow growing and grazing resistant (Dauta 1982; Sommer 1983; Horne and Goldman 1994).

Population and first derivative data at coarse taxonomic resolution—Developing a system-level tool for study of HAB population dynamics and ecosystem stability in lake ecosystems that is based on phytoplankton succession and diversity at coarse taxonomic resolution might not be practical given the limitations of existing technology. The use of many sensors deployed on moorings or by combining data from multiple overflights with airborne optical sensors will produce a data set of high temporal resolution necessary for the more powerful second derivative index (i.e., increasing the sensitivity of the tool). But incorporation of absorption data only into a classification scheme will not allow for adequate discrimination between phytoplankton groups, as indicated by the grouped Hartbeespoort Dam data.

As suggested previously, a classification scheme might become more useful with the inclusion of spectral scatter properties (Roelke et al. 1999b). In the case of the Hartbeespoort Dam data, during the fifth year, the green algae *O. lacustris*, *C. microporum*, and *S. linearis* showed highly dynamic succession patterns. But when these species were coarsely grouped as green algae, the high dynamics were lost, as well as the delineation of diversity. Inclusion of scatter properties

into the discriminant analysis might have allowed for the separation of these green algal species. For example, *O. lacustris*, *C. microporum*, and *S. linearis* differ in both size and shape considerably, and it is likely that their scatter properties also differ. The use of absorption and scatter properties might have allowed for better discrimination of the green algae, which in the case of the *M. aeruginosa* blooms in Hartbeespoort Dam would have made this potential system-level tool more practical.

An alternative to using inherent optical properties to delineate phytoplankton community composition is to observe cell characteristics (i.e., size and shape) directly and in situ. Submersible flow cytometry technology (Fluid Imaging Technologies) that provides images of phytoplankton cells is now becoming available. Access to such information will allow a more detailed classification of related algae (e.g., enumeration of *O. lacustris*, *C. microporum*, and *S. linearis* from the Hartbeespoort data) and might prove invaluable for potential system-level tools such as the one outlined here.

A proposed system-level tool for the study of HAB population dynamics and ecosystem stability in lakes, based on the dynamics of phytoplankton succession coupled to species diversity during nonbloom periods, worked well for *M. aeruginosa* blooms in Hartbeespoort Dam. There is a need, however, to further test *M. aeruginosa*, as well as other HAB species, blooms in other lake ecosystems before the utility of this tool can be fully evaluated. The derivative-based conceptual model depicting processes that influence succession dynamics and bloom initiation provided a good framework for development of this potential system-level tool.

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