A COMPUTER SIMULATION OF THE INVASION OF THE EXOTIC TREE SPECIES *MELALEUCA QUINQUENERVIA* IN SOUTH FLORIDA

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The Exotic *Melaleuca* in South Florida

The 65,000 km. encompassing the seven south Florida counties of Broward, Collier, Dade, Hendry, Lee, Monroe, and Palm Beach are currently experiencing an "invasion" of the exotic tree species, *Melaleuca quinquenervia* (Cav.) Blake. Since its introduction in the early part of this century, (Fig. 1) *M. quinquenervia* has become a significant vegetative entity in four of the south Florida counties (Broward, Dade, Lee, Palm Beach)(Fig. 2). As the spread of this species is coupled with a dimunition of native vegetation, many area residents and officials have classified the tree as a pest, worthy of Viet Nam era herbicides to bring the invasion under control. Such treatment assumes that *M. Quinquenervia* is responsible for the demise of the indigenous vegetation. To the contrary, Myers (1) has confirmed that the species does not displace vegetation in a pathological sense but that it will colonize sites where the existing vegetation has been disturbed. Regardless of the mechanism, the texture of the south Florida landscape is undergoing a change that has major implications for such activities as water management; agriculture; natural resource and wildlife management; and recreation. At this point in time, the future extent of *M. quinquenervia* and its ultimate impact on the south Florida environment are unknown.

Purpose of Research

As many questions concerning the continued spread of *M. quinquenervia* in south Florida remain unanswered, the purpose of this research is to develop a framework for the study of the dynamic and spatial behavior of the species that can be useful to investigators and planners in assessing strategies to deal with the myriad of environmental problems in which it may play a significant role.

Objective of Research

To synthesize the current knowledge of *M. quinquenervia* in south Florida and to develop a format in which the spread of the species can be evaluated, a systems approach is employed to integrate the diverse sources and fields of information in a conceptual model identifying the major interactions with the ecosystems and driving forces of south Florida. The model is then adapted for computer simulation to yield information regarding the future trends of expansion under a variety of environmental conditions. In addition, a review of the model is undertaken to suggest areas of research that would be beneficial in refining the understanding of the behavior of the species as a naturalized exotic.

To provide the information necessary for the formulation of a credible model, three main areas concerning *M. quinquenervia* are reviewed. These areas are respectively: information regarding the species' description, its host environment, and its distribution and rate of expansion. More precisely, the species' description includes a review of the ecology and morphology while the environmental review is detailed to distinguish between natural and man-initiated factors. Further subdivision of man's influence is delineated into direct and indirect interactions, with the direct interaction narrative exploring the traditional and aspiring uses of the species that led to its introduction into south Florida.

Ecology and Morphology of *M. quinquenervia*

Both Meskimen (2) and Myers (1) have reviewed the taxonomy, ecology, and morphology of *M. quinquenervia*. The following narrative is a summary of the fundamental information.

M. quinquenervia is one of 130 species included in the genus *Melaleuca*. The genus *Melaleuca* is a member of the large tropical family Myrtaceae which also includes the genera *Eucalyptus, Callistemon,* and *Psidium* among 80 other genera. Previously described as *Melaleuca leucadendron* Linn, *M. quinquenervia* is the only species of *Melaleuca* that is not a native of Australia and it is the only species of *Melaleuca* that has successfully colonized in south Florida. *Melaleuca* can be distinguished from the *Callistemon* (bottle brush) by its bundled stamens while the bottle-brush stamens are free. It also can be differentiated from *Eucalyptus* by the presence of flower petals that are absent in the eucalyptus. It has many common names including cajeput, cajuput, cajaput, punk tree, swamp tea tree, brown tea tree, paper-bark tree, broad leaved tea tree, white tea tree, white bottlebrush, whitewood, and milkwood. In south Florida it is also commonly referred to by its genus name as *Melaleuca*.

M. quinquenervia has been identified in Australia, New Caledonia, Borneo, Java, Burma, Malaysia, and Viet Nam. It has been naturalized in the Philipines, India, Madagascar, Zaire, and Hawaii. In North America, the species is found in Texas, California, and Florida.

Morphologically, *M. quinqueneriva* can assume many different growth forms, shapes, and sizes at maturity. Variations in form range from erect and cone-crowned to gnarled with pendulous branching. Its mature height has been described as between 12 to 30 m. with broadly lance-shaped leaves with three to seven paralled veins, 5 to 8 cm. long, or narrow lance-shaped leaves up to 20 cm. long. The bark has been described as resembling many layers of creamy tissue paper in a tattered and torn condition. Its wood is noted as being compact, even, fine, and short grained with a pale pinky-brown hue. The flowers of this species are creamy white in color and grouped into bottle-brush spikes from 3 to 12 cm. long with each spike containing 20 to 70 flowers. These spikes appear on the terminal ends of branches with new leaves and branch growth appearing after flowering.

In the south Florida environment, *M. quinquenervia* has been known to bloom as many as five times in a single year with individual branches supporting as many as three blooms annually. In general, the number of flowers is greatest during the wet season, extending from June through November, and least during the dry season from December through May. Some trees are known to flower during their first year.

After flowering is complete and the pistils, stamens, and petals have fallen the bottle-brush formation that remains supports some 30 to 70 pill-shaped seed capsules containing from 200 to 300 seeds each. Since the flowers are always produced on the terminal ends of twigs, the seed capsules provide a record of branch growth with 8 to 12 seed crops on a single branch not uncommon.

Within the seed capsules, the minute seeds (34,000/g) can maintain viability for several years. Research conducted by Meskimen (2) revealed that seed release occurs when the vascular connection between the seed capsule and the tree is broken. The resulting desiccation from water loss then opens the seed capsule and the seeds are free to fall out. The drying action of fire can trigger the same response as seed capsules have been observed to open within one day after exposure to fire. Meskimen found that a single tree could contain almost three million seeds resulting in prodigious seedling production after a moderate burn.

In addition to this fire-triggered seed release mechanism, *M. quinquenervia* possesses several other adaptations which provide some protection from various forms of stress. Most significant is its ability to initiate new growth from damaged and dying structures. Fire and frost damage to seedlings result in new shoots sprouting from various points along a stem. When a *M. quinquenervia* tree is felled and the trunk completely severed, shoots will coppice from the stump usually resulting in several hardy stems. The severed portion of the tree dries out and activates the seed release mechanism eventually carpeting the area with germinated seedlings. On felled trees that are not completely severed from the root structure, erect sprouts arise from the prostrate trunk which are capable of normal growth and development. In addition to its ability to vegetatively regenerate, the bark structure of the species is extremely fire resistant. The bark itself is not fire resistent but its many layers allow the outside sheets to burn without any damage to the inside layers or underlying wood. Fire damage rarely extends more than a few millimeters into the bole.

M. quinquenervia is also tolerant to flooding. On sites that are wet part of the year, adventitious roots can be produced from any vegetative organ under prolonged contact with water. This ability permits aerobic respiration in an otherwise possibly anaerobic environment. Flood water also acts as a mechanism for seed dispersion.

As its seeds are quite small and have an insignificant endocarp, dispersed seeds must germinate rather rapidly and thus the conditions of germination are critical. Meskimen (2) found the most favorable germination conditions to exist after a fire and in open sunlight on water-logged, acidic soils. Further investigation by Myers (1) has shown that areas with periodic, shallow surface flooding during the wet season tend to be more suitable for *M. quinquenervia* establishment. Seedlings were also shown to be capable of surviving several months of inundation.

Although not a native of Australia, the Australian climate is typical of the conditions to which the species is best adapted. The monsoon type climate occurs between 25° and 35° south latitude and is generally sub-humid to humid tropical climate notable for the distinct and severe wet and dry seasons. The mean annual precipitation ranges from 900 to 1300 mm and the mean annual pan evaporation is in the 1500 to 2500 mm range. The mean winter temperature in June and July (southern hemisphere) ranges from 21°C to 24°C with mean summer temperatures in December and January varying from 26°C to 30°C.

In summary, the features of *M. quinquenervia* that effectively insure its survival against the damage of flood, fire, frost, and cutting make the tree a hardy species in the harsh climates of its native range and difficult to eradicate in milder climates where it has become established. Its expansion as an exotic species is limited to areas where the native vegetation has been disturbed. In contrast, direct competition with other species is reported not to be a successful mechanism for range expansion.

Natural Features of south Florida

To aid in understanding the spread of *M. quinquenervia* in south Florida, a description of the natural features and vegetation is essential. Davis (3) has compiled a classic work on this subject which provides the basis for the following summary.

The area, generally described as south Florida, extends from the coastal plains of the Atlantic and Gulf of Mexico (the Eastern and Western Flatlands) and southward from Lake Okeechobee. The area is of very low elevation and has a flat topography. South Florida is characterized by open pine flatwoods dominated by Pinus elliotii (slash pine) and extensive areas of Palmetto or grasses known as wet or dry prairies, depending on the degree of flooding during the wet season. The otherwise homogeneous flatwoods and praries are broken by cypress domes, sloughs, hardwood hammocks, and marshes. Moving southward on the Western Flatlands, the vegetation becomes increasingly wet as the cypress swamps and wet prairies of the Everglades Basin and the area known as Big Cypress Swamp are approached. The Eastern Flatlands do not extend as far south as the Western Flatlands although the coastal ridges of the Atlantic Coast Strip and Miami Rock Ridge have fingers that lead down to Dade County and act to separate the Everglades Basin from the Atlantic Ocean. It is on these ridges where most of the intensive urban development in south Florida has taken place.

The northern and central Everglades, underlain by rough, uneven limestone deposits, is poorly drained of the floodwaters received from Lake Okeechobee during the wet season. Historically this area is flooded all year round and the extensive saw grass marshes that have developed there have contributed to the formation of thick peak and muck soils from generations of water-logged saw grass decay. Further south, the porosity of the Miami oolite formation is relatively well drained and thus flood waters draining to the aquifer during the dry season prevents the formation of marshes and thus peat and muck soils are not found in this area.

In the subtropical climate of south Florida, the six month rainy season extending from May through October normally delivers three or four times as much rain as in the dry season from November through April. Rainfall is also not distributed uniformly throughout the area. The coastal strip from West Palm Beach to Miami normally receives 1525 to 1650 mm of rain per year while the interior covering the Everglades Basin and Lake Okeechobee averages 1400 mm proceeding south to Key West, mean annual rainfall decreses to less than 1015 mm.

Closely related to the water regime are temperature and fire patterns. Temperature variations are not as extreme as the rainfall variations, with the difference between the average minimum temperatures of the hottest and coldest months being 11°C at Ft. Myers and only 9°C at Homestead. Freezing temperatures may occur any time from November through February. For the entire area, summer daily maximum temperatures rarely exceed 34°C and may have little effect on the prevailing vegetation.

Fire has always been part of the natural pattern in south Florida. Naturally triggered by lightening, it has historically played a role in checking succession of hardwoods in the pinelands, praries, and cypress swamps. Although burning may occur at any time of the year, records from the Ft. Myers area for 1972 indicate that the distribution is not uniform with 21% of all fires occurring in March with an equal number for the summer period, June through August and 40% of all fires occurring from May through September (Myers, 1).

Alterations by Man

The ecosystems of south Florida have evolved over at least the past 10,000 years under natural conditions of drought and flood cycles. Until 1875, the area has been sparsely inhabited by Seminole indians residing primarily in the Everglades. With the advent of the railroad, access to south Florida was enhanced precipitating a hundred year period of urban growth and development. As the amount of perenially dry land was scarce, massive drainage projects were undertaken to increase the amount of inhabitable and arable land. Coupled with the drainage program, demand for water for urban and agricultural purposes has greatly altered the natural water regime in an effort to store water for use during drought periods. Efforts to manage the flow and storage of water have been severely criticized to the point that some investigators have proposed filling in the extensive network of canals and levees (Marshall, 4). At this time, continuation of canal building projects are still underway in many areas of south Florida. In any case, the net effect of the drainage and water pumping operations has been to effectively lower the level of the water table. Although more dry land is available, drought and flood variances have been accentuated. During the wet season, flooding is not as extensive as previously but is more severe. During the dry season, the desiccation of vegetation from increased drainage increases the fire frequency and continued demand for scarce water during this period has encouraged salt water intrusion in coastal areas.

This change in the water regime has effectively altered the previously natural cycle of flood and drought to the pulsing characteristics of a monsoon type climate. Under such conditions, the portion of native south Florida vegetation least able to withstand the effect of heightened flooding and accentuated drought and fire is decimated while the exotic *M. quinquenervia*, well adapted to monsoon conditions, is able to survive and assume dominance. Under such a water management program, the continued spread of the species in south Florida can be considered an environmental indicator of the alteration by man imposed on nature.

The influence of other stresses applied by man that accompany urbanization including air, water, noise, and thermal pollution along with increased direct pertubation of natural areas by logging, hunting, boating, and road building is more difficult to evaluate in terms of the effects on the distribution and composition of the vegetation.

Energy Modelling

The basis for the systems approach is the formulation of a model that provides a synthesis of knowledge of the system under consideration. In its broadest sense, the model is a translation of reality into a symbolic language than can be viewed from a common perspective. Such translations enable phenomena at diverse scales and degrees of complexity to be analyzed and compared utilizing a singular set of investigative tools. However, as in any translation, care must be taken to insure consistency and the preservation of original structure relationships. Of the modelling languages available, the energy circuit language developed by Odum (5) provides the consistency of form required to accomplish these tasks.

The versatility of energy circuit language stems from its reliance on thermodynamic principles that are included in all its model formulations. Thus besides the conservation of matter fundamental to Forrester's technique (6), energy circuit language also requires conservation of energy thus reducing the amount of arbitrary functions required to link dissimilar flows and storages. As all energy flows must be accounted for, the completeness of the model can be insured by "auditing" the model's pathways for an appropriate energy balance. Provision is also made to incorporate the concepts of energy source and energy stress as actions that tend to increase or decrease energy storages, respectively.

Theoretical Considerations

The energy approach to system modelling as developed by Odum (5) is based on the assumption that analysis of the energy flows through a system provides the best information of the fundamental structure and characteristics of that system. In this approach, the flow of energy is traced from "upstream" sources of potential energy to energy processors that constitute the main system structure. Further downstream, the flow of energy is followed to its ultimate site of disposal where its capacity to perform any additional work is exhausted. In addition to adherence of the thermodynamic laws of energy conservation and degradation, the energy approach incorporates a system principle developed by Lotka (6) in which system structure and organization are assumed to develop in a manner amenable to processing available energy at the maximum possible rate for the production of useful work. To accomplish this task, the system must expend a portion of its upgraded processed energy in excess of the energy required for the "speed tax" of the energy degradation law and return it upstream to interact with its exogenous energy sources. The limit of the rate at which energy can be upgraded in such a process to perform useful work on a long term basis is constrained by the requirement that the sum of the energy fed back upstream, the energy required for maintenance of system structure (respiration), and energy dissipated through other pathways cannot exceed the rate of upgraded energy production. These relationships are diagrammed in the self maintaining module depicted in Fig. 3 utilizing the symbols of energy circuit language. A description of energy circuit language symbols are provided in Fig. 4. Although it is hypothesized that these pathways exist in all stable systems, it is often quite difficult to numerically evaluate the flows from empirical data. For the data available for the model under consideration, an analytic derivation follows that enables the evaluation of all pathways.

Expressing the above relationships in differential equation form, the rate of change of the upgraded energy storage (Q) is the difference between the remainder of the processed energy that has not dissapated ($\frac{J}{2}$ = 50 percent of processed energy at maximum rate) and the sum of all outflowing, upgraded energy for upstream contribution to production (W) and downstream outflows for maintenance (R), export (E), harvest (H), and stress (S):

$$\frac{dQ}{dt} = \frac{J}{2} - (W + R + E + H + S) \quad (1)$$

The total production, (J) represents the flow that results from the difference in the forces exerted by the upstream energy source (1) and the backforce created by the upgraded energy storage (Q/C). This net force when interacted with the upgraded, fed back energy (W) produces the energy flow:

$$J = k_0 W(I - (Q/C)) \quad (2)$$

As (W) is proportional to the force exerted by the storage (Q), this upgraded feedback work can then be described as:

$$W = k_B(Q/C) \quad (3)$$

yielding an expression for the production as:

$$J = k_0 k_B (Q/C)(I - (Q/C)) \quad (4)$$

Similarly, the respiration and export pathways are also proportional to the force exerted by the storage such that:

$$R = k_R(Q/C) \quad (5)$$

$$E = k_E(Q/C) \quad (6)$$

Since the stress pathway is proportional to the square of storage force, the stress flow can be described as:

$$S = k_S(Q/C)^2 \quad (7)$$

Finally, as the rate of harvest is considered to be controlled externally, then it is designated as the constant (H). Thus, substituting (2)-(7) into (1) yields the quadratic expression:

$$\frac{dQ}{dt} = -[\frac{k_0 k_B}{2C^2}]Q^2 + [\frac{k_0 k_B I - 2(k_B + k_R + k_S + k_E)}{2C}]Q - H \quad (8)$$

Evaluation of this expression is possible if several assumptions are made. In the case of a vegetative system if it is assumed that the vegetation is in steady state, then the value of Q(plant biomass), R (respiration), and P (gross primary production) where

$$P = \frac{k_0 k_B (Q/C)(I - (Q/C))}{2} - \frac{k_B Q}{C} \quad (9)$$

can be empirically measured. It it is also assumed that all flows are continuous and the potential energy source (I) held constant and the coefficient k_0 representing the fraction of potential energy captured is known, then the remaining constant (C) representing storage capacity and the coefficients k_B, k_R, k_E, and k_S can be determined if several other assumptions are made. If it is assumed that the maximum production coincides with the steady state value of Q, then as a result of Lotka's principle:

$$\frac{dP}{dQ} = \frac{k_B(k_0(- 2k_0 Q - 2)}{2C} = 0 \quad (10)$$

and solving for Q yields:

$$Q = \frac{(k_0 I - 2)C}{2k_0} \quad \text{at maximum P} \quad (11)$$

assuming that i , the available potential energy, and k_0 the fraction of potential energy captured are known and that Q is also found empirically, then the value of the constant C can be found by inspection:

$$C = \frac{2Qk_0}{(k_0 I - 2)} \quad (12)$$

Similarly, the value of k_B can be found by substituting (11) into (9), yielding:

$$B = \frac{8k_0 P}{(k_0 I - 2)^2} \quad (13)$$

where P is measured empirically. The relationship between production (P) and the quantity of upgraded energy (Q) are shown in Figs. 5 and 6. Continuing, the coefficient k_R, is easily determined as:

$$k_R = RC/Q \qquad (14)$$

where the respiration (R) is measured empirically and the values of C and Q are as above. Finally, k_E, k_S, and H are found by assuming that in steady state:

$$P - R = E + S + H \qquad (15)$$

and distributing the excess of production (P) over respiration (R) among the flows export (E), stress (S) and harvest (H) based on best available estimates. It is then a simple matter to determine k_E and k_S as in (16) and (17) respectively:

$$k_E = EC/Q \qquad (16)$$

$$k_S = SC/Q \qquad (17)$$

Thus, all the coefficients and constants that describe the self-maintaining module can be completely determined for each entity in the model and concentration can then shift to the energy pathways and storages that occur between modules.

Model Description

As seen in Fig. 7 the model, diagrammed in energy circuit language, is divided into four major components or modules: mature melaleuca, melaleuca seedlings, dryland vegetation (representative of pine) and wetland vegetation (representative of cypress). Only a minimum of detail is presented for the dryland and wetland vegetation modules while the melaleuca modules are expanded to show the seed production and germination cycle. All the modules are equipped with stress pathways that act to decrease accumulated biomass when any of the stresses of drought, flood, fire or frost are in effect. The severity of the stresses is adjusted to reflect the stress tolerance of the respective modules. Each module is also driven by an energy source, which in this simulation is limited to the photoperiod of available sunlight.

In the mature melaleuca module, photosynthesis and gross primary production is represented by the interaction of the energy source with the existing level of accumulated melaleuca biomass. The resulting production is then differentiated into production of additional melaleuca biomass and production diverted for the formation of melaleuca seeds. Respiration is accounted for as a drain on biomass and a heat sink on the production multiplier. Stress pathways are also included to show the effect of the generalized stresses of drought, flood, fire and frost (see detail in lower right corner of Fig. 7). In addition to production, the mature melaleuca biomass is also increased by a pathway representing maturing melaleuca seedlings.

As melaleuca is a fire adapted species, its seed dispersal mechanism is also fire dependent. This phenomenon is represented as a pathway from the storage of seeds remaining on the trees to a storage of dispersed seeds controlled by a switch that only opens the pathway during a fire condition. The remainder of the time, the seeds on the trees accumulate from normal production and are decreased by a pathway representing seed mortality.

Those seeds that survive to become dispersed seeds are faced with further hazards before they can germinate. As in the switched dispersal pathway, the pathway leading to the germinated seed state is also controlled by a switch. However, instead of being triggered by a fire condition, the germination switch is controlled by the condition of available soil moisture. Those dispersed seeds awaiting the proper germinating conditions are exposed to environmental hazards represented by the dispersed seed mortality.

The melaleuca seedling module contains the storage of germinated seeds which is used as a counter of melaleuca seedlings. Thus, melaleuca seedling production is multiplied by the number of germinated seeds to yield total production. Likewise, the amount of melaleuca seedling biomass is decreased in proportion to normal germinated seed mortality as well as in proportion to the stress mortality applied to the germinated seed storage. The rate of seedling maturity to mature melaleuca is also controlled by a pathway from the germinated seed storage which is adjusted to account for the time delay between germination and maturity. A respiration pathway is also provided on seedling biomass to represent unit respiration.

The more generalized dryland and wetland modules are each depicted with one multiplier representing the interaction of the energy source with the accumulated biomass to produce additional biomass. Respiration and stress pathways are provided as with melaleuca. These modules are also equipped with pathways to account for the harvest by man for lumber and other purposes.

In addition to the stress pathways, competition is introduced for the available energy captured by each module. As a first approximation, energy is alloted in proportion to the relative share of each module's accumulated biomass to the total biomass at any point in time.

Model Initialization

As detailed field research is required to provide many of the values needed in the model, for the illustory purpose of this exercise determination of model values is limited to the scope of the existing data base. The primary data sources employed are Myers (1), Mitsch (8) and personal consultation with Myers. Supplemental data sources (9), (10) are listed in the references.

Computer Simulation

The second major feature of the systems approach includes the simulation of the system model. The simulation process is a means of exploring the behavior of the model by "energizing" its structure. For the type of models under consideration, this energizing is accomplished with the aid of analog computers that use electrical energy to flow through a representation of the model structure directly, or digital computers that use discrete logic mechanisms of a symbolic model interpretation to accomplish this task. The advantage of the simulation process is that non-destructive testing of the model structure can be performed many times to determine the response of the model under a variety of representative conditions.

The selection of analog or digital technique depends on the nature and complexity of the model. Analog simulation provides a relatively fast method of executing models of limited complexity. It also has the distinct advantage of modifying the model structure (adjusting coefficients and initial conditions) with a minimum of difficulty to check the sensitivity or change the conditions of the simulation. Digital simulation has the advantage of accommodating much larger models although changes in conditions or sensitivity testing must be executed in much slower sequential process. For the purposes of the models to be developed in this research, the complexity requires the use of the digital simulation process.

Results

The model was subjected to a combination of stresses representative of the natural program of fire, flood, frost and drought. As the effect of these applied stresses is not explicitly known, the stress coefficients of each module were adjusted until a stable pattern of melaleuca, dryland and wetland vegetation was generated (8). With this accomplished, the effect of modifying the natural stresses to resemble a monsoon type climate (a stress program with sharp wet and dry periods) was noted when this new combination of stresses was applied to the model. These results are depicted in Fig. 9. As can be noted by comparing Figs. 8 and 9, melaleuca is able to take advantage of the increased stress mortality on dryland and wetland vegetation and increase its biomass at the expense of the native vegetation. In one simulation melaleuca increased from a relative one percent of total vegetation to over forty percent of total vegetation. Also of note is the fact that once the stress coefficients of the various components were established no combination of stresses could reduce the amount of existing melaleuca without a corresponding decrease in native vegetation. Thus, it would appear from these preliminary results that melaleuca will remain a fixture of the south Florida landscape for some time to come (Note: Detailed results of the simulation and results are discussed in Sedlik (11)).

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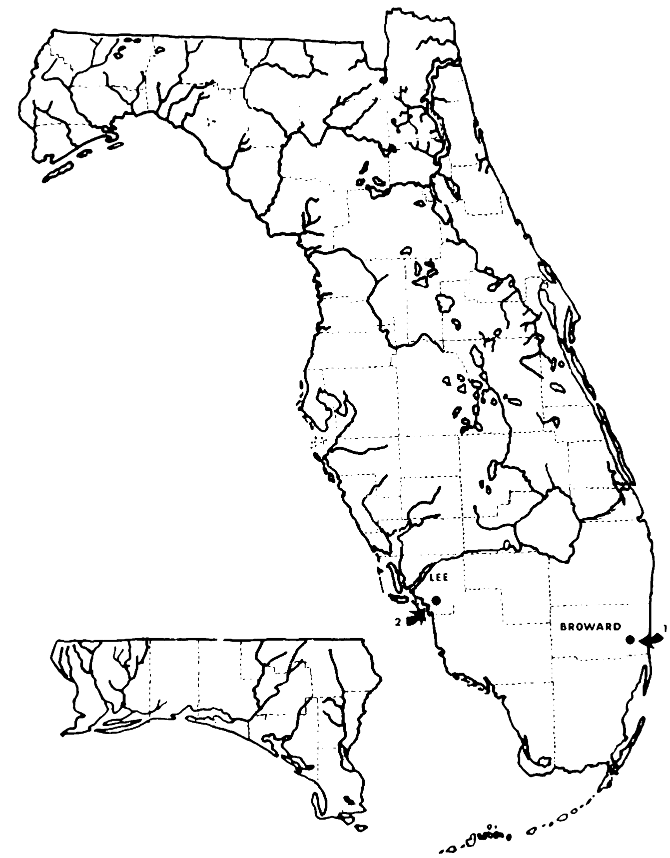


Fig. 1 Sites of original introduction of *M. quinquenervia* in south Florida (ca. 1920). Source: Myers (1)

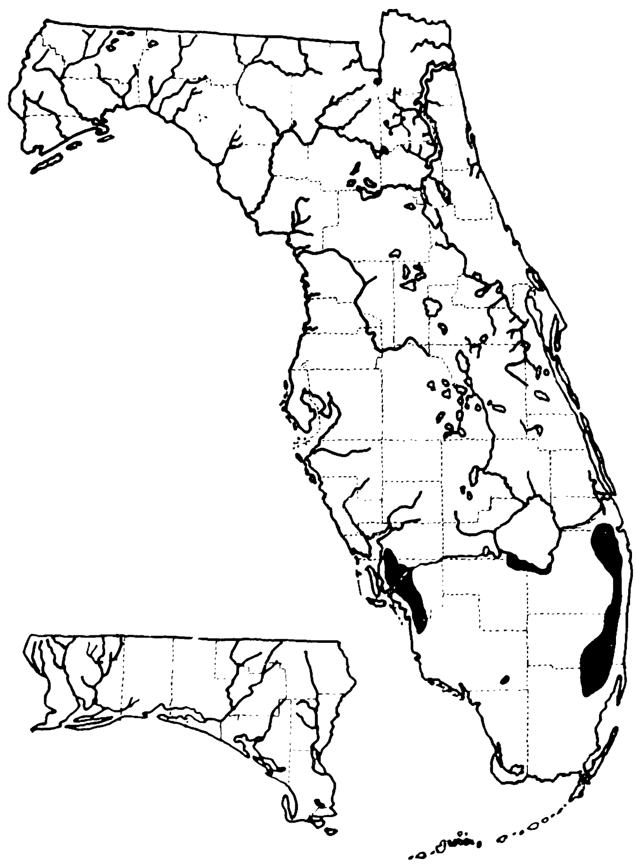


Fig. 2 Current approximate distribution (1975) of *M. quinquenervia* in south Florida.
Source: Myers (1)

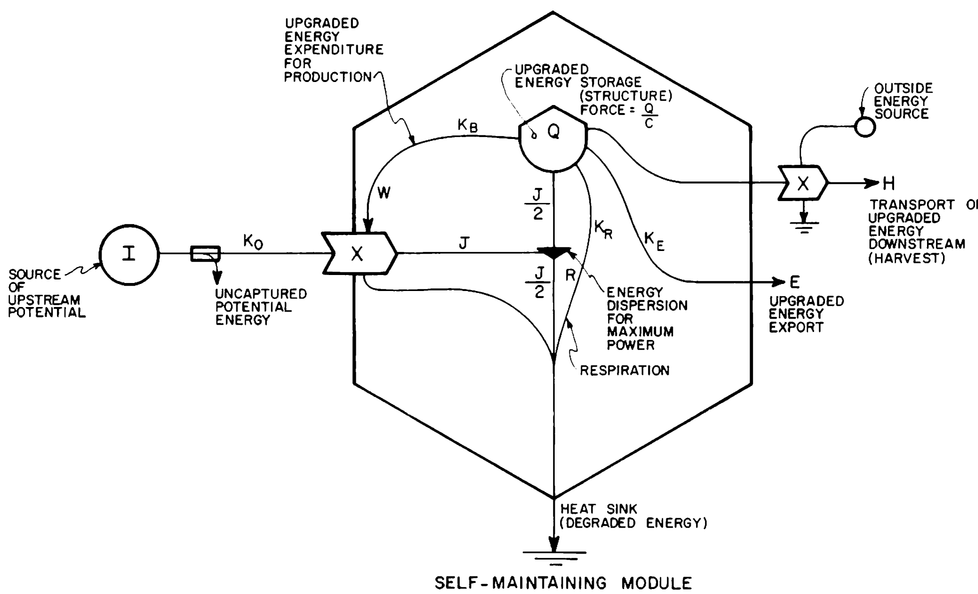
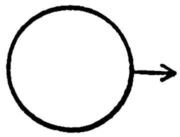


Fig. 3 Energy circuit language self-maintaining module as developed by Odum (5).

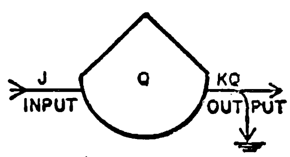


SOURCE

(a) External, unlimited energy source to the system.

HEAT SINK

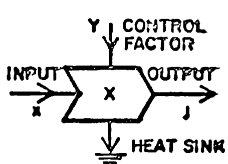
(b) Heat sink as required by the second law of thermodynamics in order to do work.



$\dot{Q} = J - KQ$

PASSIVE STORAGE

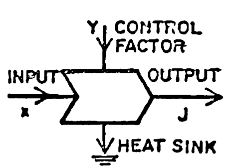
(c) Component of energy or matter storage in which quantity stored is the integral of the inflows and outflows.



$J = KXY$

MULTIPLIER

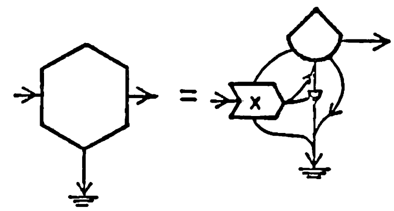
(d) Interaction in which output is proportional to the product of two input forces.



$J = f(X,Y)$

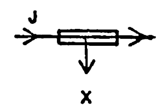
GENERALIZED WORKGATE

(e) Interaction in which output is some unspecified function of two input forces.



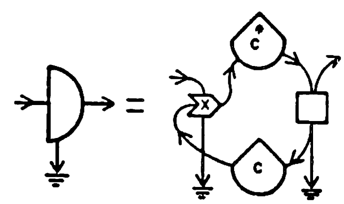
SELF MAINTAINING CONSUMER UNIT

(f) Autocatalytic unit which by virtue of feedback mechanisms may enhance its ability to process energy.



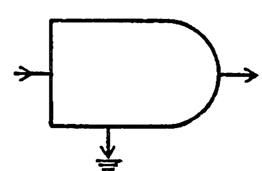
FORCE FROM A FLOW

(g) Force (X) acting in proportion to flow (J).



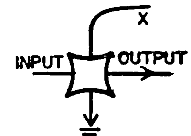
CYCLING RECEPTOR

(h) Cycling receptor module as in chlorophyll excitation-deactivation cyles and other anabolism.



GREEN PLANT AND OTHER PRODUCERS

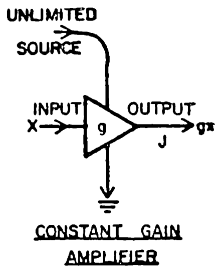
(i) Autotrophic individual or community which has both anabolic and catabolic processes.



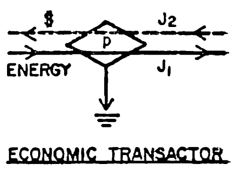
DIGITAL FUNCTIONS

(j) Switch used when flows are regulated by on-off signals such as lake regulation or political decisions.

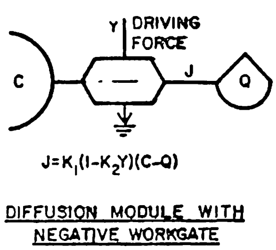
Fig. 4 Description of Energese, an energy circuit language used for modeling in this study (Odum, 1971, 1972).



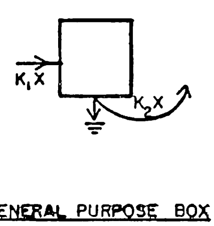
(k) Constant gain amplifier used when unlimited source drives low flow without affecting the source.



(l) Economic transactor showing opposite flow of money and energy.



(m) Two-way workgate which operates according to the gradient and driving force.



(n) Box used to lump linear processes. Nutrients can be shown being recycled from respiratory pathways.

Fig. 4 (cont.)

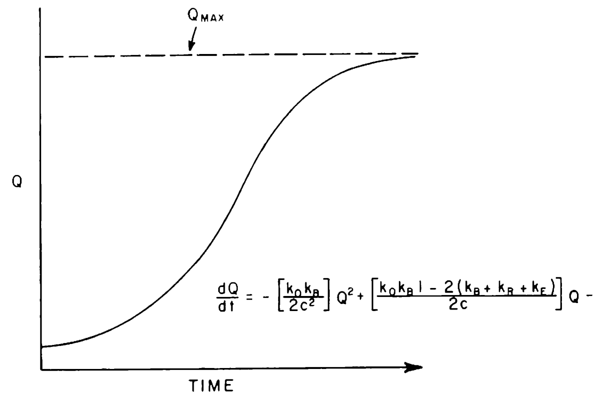


Fig. 5 Logistic growth pattern of upgraded energy storage obtained from self-maintaining module.

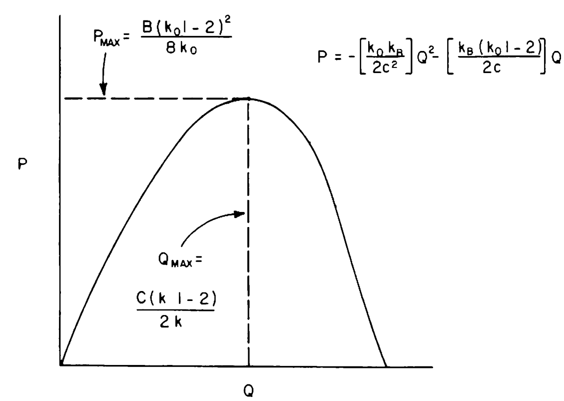


Fig. 6 Production function of upgraded energy storage. Natural systems, according to Lotka's principle will evolve to maximize production in steady state.

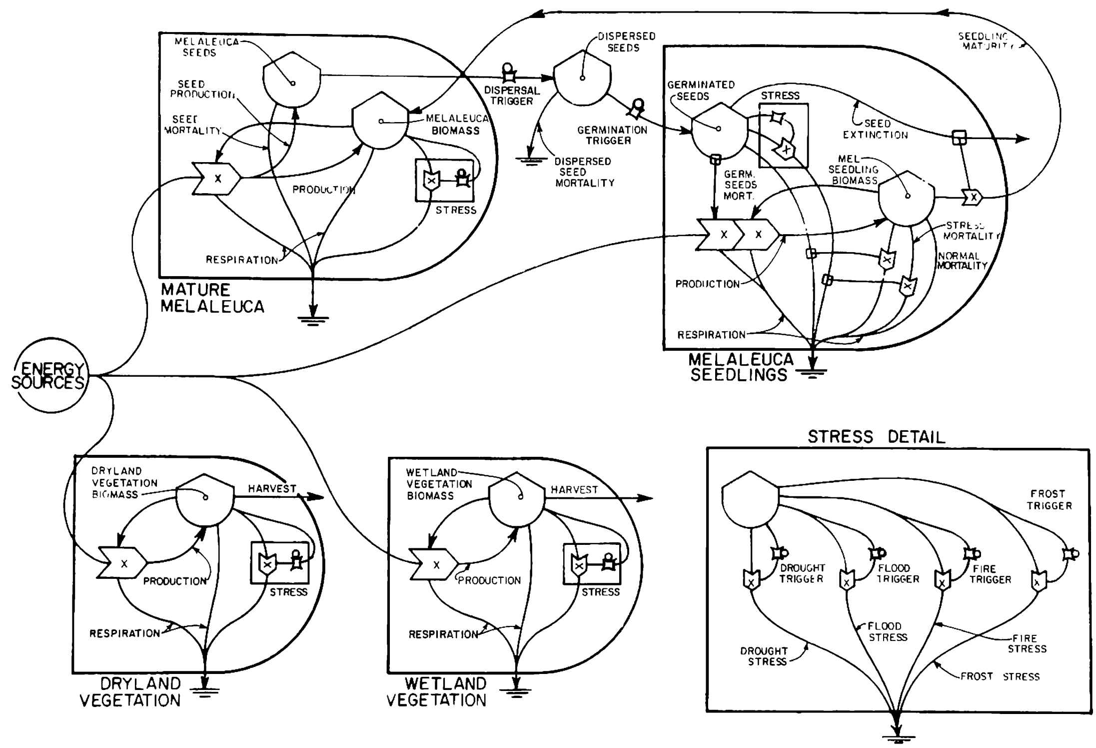


Fig. 7 Energy circuit language model of *M. quinquenervia* in south Florida.

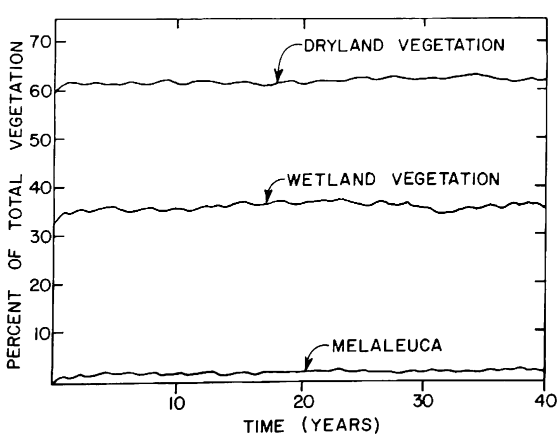


Fig. 8 Response of melaleuca model in steady state under original south Florida environmental conditions.

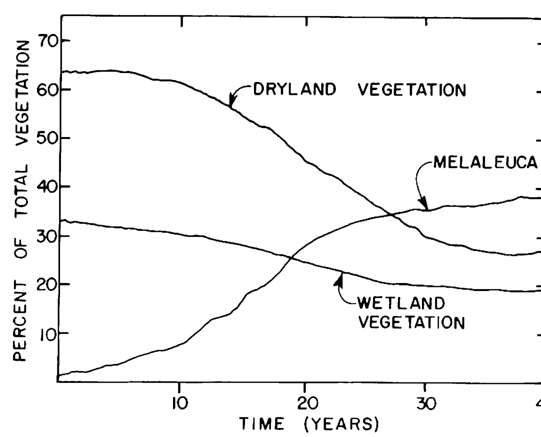


Fig. 9 Response of melaleuca model when subjected to monsoon type climatic environment (severe wet and dry periods).