VEGETATIVE PROPAGATION AND MODEL STRUCTURES

 Definitions and rule description of vegetative propagation

Initial efforts focused on the development of generic multiplication models applicable for a variety of vegetative propagation methods. Fig. 1 shows an example of vegetative propagation starting with a single-node cutting with one leaf. The propagation process is sometimes followed by a transplant finishing process (rooting or hardening stage) before shipping (not shown in Fig. 1). The following propagation definitions and statements will be used. They are applicable to most vegetative propagation systems, including micropropagation and macro-propagation for transplant production.

1) Propagules are plant tissues or organs that can be used as starting materials for propagation (propagule production).
2) Stock plants are plants grown in order to produce propagules. Their status (stage) of maturity, whether ready to be harvested or not, is irrelevant to the definition of stock plants. Even cuttings that have just been planted in the propagation system can be referred to as stock plants.
3) Propagation cycle (Tc) is the duration of time required for stock plants to grow and produce new propagules.
4) Since multiplication rates are class-dependent and more than one class (kind) of propagule can be used for propagation, propagules are often classified, e.g., as cutting and stock plant base [the base of the stock plant remaining after harvesting the cuttings (Fig. 1)].
5) Propagules are further classified according to their attributes (age, size, etc.). Stock plants are classified with attributes such as days in Tc, along with the attributes of their original propagules.
6) A portion of the propagules can leave the propagation process by being either sold or transferred to the finishing stage. The rest of the harvested propagules are used for serial propagation.
7) A portion of the propagules or stock plants can be stored for growth suppression and quality preservation.
8) Propagation processing has spatial restrictions, such as areas for propagation, finishing and storage.
9) The number of propagules handled per unit time can be limited by labor availability.

Mathematical Description

Considering the ecological characteristics of vegetative propagation in a closed environment, where plants repeat their “life cycles” from propagules, continue growth as stock plants, and finally produce new propagules, a demographic approach often...
used in ecological population dynamics can be applied. As an extension to the Leslie matrix (1945), Law (1983) introduced a transition matrix model in ecological plant population dynamics. Such matrices can be applied in vegetative propagation systems, since such propagation can be expressed as a transition from propagules to stock plants and from stock plants to propagules. For developing transition matrix models, the observation interval of the transition is determined. The interval will be shorter (daily or weekly transition) in vegetative propagation than in ecological population dynamics (seasonal or annual transition). Another differing characteristic of transition matrix models for vegetative propagation is that the models can be deterministic and coefficients can be manipulated according to the production strategy (decision of a production manager), while those in the ecological transition are stochastic.

The dynamics of the number of propagules and stock plants are expressed in a simple propagation system; and 3) propagules leaving the system (for shipping or transition to the finishing stage). The population vector on day t is now expressed with three subvectors:

\[ \mathbf{N}(t) = \mathbf{P}(t); \mathbf{S}(t); \mathbf{F}(t) \]  \[ \text{(1)} \]

where \( \mathbf{P}(t) \), \( \mathbf{S}(t) \), and \( \mathbf{F}(t) \) consist of the numbers of harvested propagules, stock plants, and propagules leaving the system, respectively, on day t. They are further classified as follows:

\[ \mathbf{P}(t) = [P_{A_0}(t); P_{B_0}(t); \ldots] \]  \[ \text{(3)} \]
\[ \mathbf{S}(t) = [S_{A_0}(t); S_{A_1}(t); S_{A_2}(t); \ldots; S_{AX_{A-1}}(t); S_{B_0}(t); S_{B_1}(t); \ldots; S_{XB_{X-1}}(t)] \]  \[ \text{(4)} \]
\[ \mathbf{F}(t) = [F_{A_0}(t); F_{A_1}(t); \ldots] \]  \[ \text{(5)} \]

where \( P_{A_0}(t) \), \( P_{B_0}(t) \), \ldots and \( F_{A_0}(t) \), \( F_{A_1}(t) \), \ldots are numbers of harvested (P) and leaving (F) propagules classified into A, B, \ldots and grown for \( x \) d \( [x < X_A \text{ for } S_{A_0}(t); x < X_B \text{ for } S_{B_0}(t); \ldots] \) in \( T \). According to the propagation rules, the number of each population constituent on day \( t+1 \) can be written as follows:

\[ \begin{align*}
\mathbf{P}(t+1) &= \mathbf{M}_{AP} \cdot \mathbf{S}(t) \\
\mathbf{S}(t+1) &= \mathbf{M}_{SP} \cdot \mathbf{P}(t) + \mathbf{M}_{SS} \cdot \mathbf{S}(t) \\
\mathbf{F}(t+1) &= \mathbf{M}_{FP} \cdot \mathbf{S}(t)
\end{align*} \]  \[ \text{(6)} \]

where \( \mathbf{M}_{AP} \), \( \mathbf{M}_{SP} \), and \( \mathbf{M}_{SS} \) are the multiplication and transition submatrices, consisting of multiplication and transition parameters from stock plants on day \( t \) to propagules on day \( t+1 \), from propagules on day \( t \) to stock plants on day \( t+1 \), and from stock plants on day \( t \) to stock plants on day \( t+1 \), respectively. \( \mathbf{M}_{AP} \) is the submatrix, including parameters responsible for the decision regarding the ratios of the number of propagules leaving the system over the harvested propagules from stock plants. Parameters contained in the multiplication submatrices \( \mathbf{M}_{AP} \) and \( \mathbf{M}_{SS} \) can be expressed as functions, including variables reflecting environmental conditions, such as air temperature, \( PPF \), and \( CO_2 \) concentration. The Eq. [6] are re-written in matrix notation as in Eq. [7].

\[ \begin{bmatrix}
\mathbf{P}(t+1) \\
\mathbf{S}(t+1) \\
\mathbf{F}(t+1)
\end{bmatrix} =
\begin{bmatrix}
\mathbf{M}_{AP} & 0 & 0 \\
\mathbf{M}_{SP} & \mathbf{M}_{SS} & 0 \\
0 & \mathbf{M}_{FP} & 0
\end{bmatrix}
\begin{bmatrix}
\mathbf{P}(t) \\
\mathbf{S}(t) \\
\mathbf{F}(t)
\end{bmatrix} \]  \[ \text{(7)} \]

Using Eqs. [2], [3], [4], [5], and [7], we can simulate the number of each population constituent and its dynamics. Once the propagation process is quantitatively understood, several important variables can be derived for considering propagation efficiency. For example, the total number of stock plants currently present in the propagation area TTL(t) is derived as:

\[ \text{TTL}(t) = \sum_{x=0}^{X_A-1} S_{AX_x}(t) + \sum_{x=0}^{X_B-1} S_{BX_x}(t) \]  \[ \text{(8)} \]

The TTL(t) is necessary for considering the limitation of capacity in a propagation system. For example, based on \( \mathbf{F}(t) \) and TTL(t), a productivity (PRDT, the number of final
propagules divided by the total number of stock plants present in the production area on the previous day) is shown as:

$$\text{PRDT}(t) = \frac{F(t)}{TTL(t-1)}$$  \[9\]

PRDT(t) is shown as a vector in this equation since F(t) is a vector. Variables such as TTL(t) and PRDT(t) will be used in analyzing the propagation process, and they will serve important roles in optimizing it.

**AN APPLICATION OF THE MODELS TO SWEETPOTATO [IPOMOEA BATATAS (L.3)] TRANSPLANT PRODUCTION UNDER CONTROLLED ENVIRONMENTS**

The generic models described above (Eqs. [1] to [9]) were applied, with necessary modifications, to sweetpotato vegetative propagation (cutting production) under a controlled environment. Sweetpotato is an important crop in many Asian and African countries, and will contribute to food, energy, and plastics production in the 21st century (Kozai et al., 1996).

Axillary shoot cuttings with several leaves have been commonly used as propagules in conventional sweetpotato propagation; in most cases, this is carried out in screen houses to prevent stock plants from reinfection with viruses carried by insect vectors. The use of single-node, leafy cuttings as propagules has been considered unsuitable because of the low survival and growth rates under environmental conditions of conventional propagation systems. However, it may be suitable under controlled environment with artificial lighting, since environmental conditions can be manipulated to achieve a high percentage of survival of single-node cuttings and high growth/development rates of the new axillary shoots. Furthermore, simulation has shown that more transplants can be obtained during a given propagation period (Tc) when single-node, rather than multi-node, cuttings are used as propagules (unpublished data). In the present study, single-node, leafy cuttings were used as propagules. Each stock plant had several leaves on its single axillary shoot, and was divided at the end of the propagation cycle into single node cuttings, each with one leaf.

**Number of propagules obtained in a propagation cycle**

Axillary shoot development from a single-node cutting is largely controlled by environmental conditions. Thus, leaf development rates, expressed as functions of environmental factors, primarily determine the number of propagules obtained per stock plant. Such rates should take into account the number of leaves usable as propagules. Preliminary experiments have shown that the number of sweetpotato single-node cuttings produced per stock plant [PcSc(t)] increases linearly after a lag time:

$$PcSc(t) = 1 + \frac{(t - t_d)}{t_p}$$  \[10\]

where t is days after planting the propagules, t0 is days to produce the first leaf usable as a propagule, and t0 is the constant interval in days between production of two successive leaves usable as propagules. The t0 and t0 values can be expressed as functions of environmental variables. A constant interval between emergence of two successive leaves larger than a standard leaf has been defined as a plastochron (Erickson and Michelini, 1957). In the present study, leaves larger than the initial leaf of the original propagules were considered to be usable as propagules.

**Model descriptions for propagule production**

Another class of propagule (other than cuttings) that is often used in sweetpotato propagation is stock plant bases (basal, rooted part of the stock plants left after removal of the axillary shoots). After cuttings have been harvested, stock plant bases, with or without their lowest, newly developed leaves, may be retained in propagation for regenerating new axillary shoots. Such bases are generally considered to have higher multiplication rates than cuttings, and their propagation cycle can therefore be shorter. The same bases can be repeatedly used to produce cuttings. They will be discarded after a maximum number of repetitions (K, K = 1, 2, 3, …). Thus the population vector for sweetpotato propagation considers two classes of propagules and two classes of stock plant bases originating from either propagule class, as in Eq. [11]:

$$N(t) = [Pc(t); Pd(t); Dd(t); Sb(t); Sc(t); Fc(t)]$$  \[11\]

where Pd(t), Fd(t), and Sc(t) are subvectors containing numbers of single-node cuttings, stock plant bases, and final single-node cuttings (those leaving the propagation system) on day t, respectively, each classified with a set of attributes (age, size, etc.). Dd(t) is the number of discarded stock plant bases on day t. Sc(t) and Sb(t) are subvectors containing numbers of stock plants originating from single-node cuttings and stock plant bases, respectively, and continue in the propagation system. Optimum duration of Tc and maximum number of repetitions (K) for using the same stock plant bases could be determined through optimization of the production process. The N(t+1) is given by multiplication of a square matrix M and N(t) as shown in Eq. [1].

The multiplication matrix M for sweetpotato propagation is written as:

$$M = \begin{bmatrix} 0 & 0 & 0 & M_{ScC} & M_{ScC} & 0 \\ 0 & 0 & 0 & M_{ScB} & M_{ScB} & 0 \\ 0 & 0 & 0 & 0 & M_{ScB} & 0 \\ 0 & 0 & 0 & M_{ScSb} & M_{ScSb} & 0 \\ 0 & 0 & 0 & M_{ScSb} & M_{ScSb} & 0 \\ 0 & 0 & 0 & M_{ScMc} & M_{ScMc} & 0 \end{bmatrix}$$  \[12\]

where $$M_{ScC}$$, $$M_{ScB}$$, $$M_{ScSb}$$, and $$M_{ScMc}$$ are multiplication submatrices containing multiplication and transition parameters from one population constituent to another in the population vector. Subscript letters represent stock plant bases (Sb), cuttings (C), stock plant bases (B), discarded stock plant bases (D), and finished cuttings leaving the system (F). The order of the letters indicates the direction of transition from day t to day t+1; for example, $$M_{ScC}$$ is the multiplication matrix from a stock plant originating from cuttings on day t to cuttings on day t+1.

**Simulation of propagation**

The models and parameters were incorporated, and simulations were conducted using MATLAB (Ver. 5.2, The Math Works, Natick, Mass.) run on a personal computer. To simplify the results, constraints of production were not considered in the present simulations. All the cuttings were considered to have identical multiplication rates, as were stock plant bases within their K value limit. Thus, Pd(t) and Sc(t) were considered as numbers (not as vectors). Sc(t) had an attribute of days in Tc, $$Pd(t)$$ had K value, and Sb(t) had attributes of Tc and K in the present simulations. The simulations were based on the following two scenarios for examining the effects of a ratio of Pd(t) and Sc(t) [α(t) = Pd(t) / Sc(t)], environmental conditions, and propagation methods (propagation with or without stock plant bases as propagules in addition to cuttings).

Simulation of numbers of population constituents of vegetative propagation as affected by α(t) values (Scenario #1). Both cuttings and stock plant bases were used as propagules. Each stock plant derived from a cutting and a stock plant base produced five cuttings and one stock plant base after 20 and 12 d, respectively, in one environment (details of the environmental conditions are not defined for this simulation). The K value of a stock plant base was fixed as K = 3. The ratio of number of cuttings leaving the system to that of cuttings harvested on day t [α(t): 0 ≤ α(t) ≤ 1] was varied. The α(t) could be manipulated dynamically but it was considered to have a constant value for the Tc examined [α(t) = 0.05, 0.2, 0.5, and 0.95, 0 ≤ t ≤ 100]. Propagation started with 500 cuttings that were planted in transplant trays on day 0.

Fig. 2 shows the four variables, Pd(t), Pd(t), Dd(t), and TTL(t), simulated for 0 ≤ t ≤ 100 at α(t) = 0.05, 0.2, 0.5, and 0.95. As was observed in real propagation operations (and therefore, as was expected), smaller α(t) gave greater values in Pd(t) and TTL(t). At α(t) = 0.95, the maximum values of TTL(t), Pd(t), and S(t) seemed stable, regardless of the discrete variations. The discrete distribution of production was the result of the different Tc for two classes of propagules. The integrated Pd(t) for 1 ≤ t ≤ 100 (integrated number of the cuttings that left the propagation system for 100 d) at α(t) = 0.05 was 1.96 × 10^8, 9.1 times as great as at α(t) = 0.95 (2.16 × 10^8). The TTL(t) remained greater than Pd(t)
at $\alpha(t) = 0.5$ or lower, while the TTL(t) was mostly lower than $F_c(t)$ at $\alpha(t) = 0.95$, reflecting the increase in the PRDT(t) with increasing $\alpha(t)$ values. For commercial propagation, the TTL(t) should be constant within a certain range satisfying spatial limit. The $F_c(t)$ should be high enough to meet the market demands, and ideally should be constant. The present simulation suggested that propagation should start with a low $\alpha(t)$ value to increase the number of propagules rapidly. The $\alpha(t)$ value can be increased after TTL(t) or $P_c(t)$ has reached ideal ranges, which will be determined through optimization processes. The ideal $\alpha(t)$ values depend on multiplication parameters and propagation cycles of different propagules. Simulation is, therefore, the useful way of finding such values and subsequently for optimizing the propagation process. Strategic introduction of short-term storage of stock plants or propagules would also contribute to optimizing the propagation process. Storage has not been considered in the present models.

**Simulation of numbers of population constituents of sweetpotato vegetative propagation as affected by use of stock plant bases as propagules under different environmental conditions (Scenario #2).** Propagation with cuttings as propagules was compared with that with both cuttings and stock plant bases as propagules ($K = 3$ for stock plant bases). Stock plants derived from cuttings and stock plant bases were grown for 20 and 12 d, respectively. The $\alpha(t)$ was fixed at $\alpha(t) = 0.8$ ($0 \leq t \leq 100$). Two sets of environmental conditions were considered: 1) high PPF ($300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), high CO$_2$ concentration ($1000 \mu\text{mol}\cdot\text{mol}^{-1}$), and high temperature ($30 \degree\text{C}$); vs. 2) low PPF ($150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), low CO$_2$ concentration ($350 \mu\text{mol}\cdot\text{mol}^{-1}$), and low temperature ($25 \degree\text{C}$). Propagation started with 500 cuttings that were planted on day 0.

A separately conducted experiment provided the parameters $t_i$ and $t_c$ in Eq. [10] as 4 and 1.3, respectively, under high PPF, high CO$_2$ concentration, and high temperature (HIGH) conditions, and as 8 and 2.0, respectively, under low PPF, low CO$_2$ concentration, and low temperature (LOW) conditions (the experimental details will be provided in a separate report). Thus, the numbers of cuttings produced per stock plant in 20 d are 13 for the HIGH conditions and 7 for the LOW conditions. Stock plant bases were considered to produce the same number of cuttings per propagation cycle as did cuttings, but with a shorter propagation cycle (12 d). Those numbers were included in the model as parameters in submatrices $M_{sc}$ and $M_{sc}$ in Eq. [12].

Fig. 3 shows the four variables, $P_c(t)$, $F_c(t)$, $D_f(t)$ and TTL(t), simulated for $0 \leq t \leq 100$ with or without usage of stock plant bases as propagules in addition to cuttings under two environmental conditions. Production of cuttings occurred every 20 d when only cuttings were used as propagules, while it had a discrete variation when stock plant bases were used in addition to cuttings. The use of stock plant bases as propagules increased the $P_c(t)$, $F_c(t)$ and TTL(t). The integrated $F_c(t)$ for 100 d ($1 \leq t \leq 100$) when both cuttings and stock plant bases were used as propagules were $3.06 \times 10^3$ and $1.62 \times 10^3$ under LOW and HIGH conditions, respectively, and 7.5 and 4.2 times as great as that when only cuttings were used as propagules under the same environmental conditions. Aitken-Christie and Jones (1987) developed a new propagation method for Pinus radiata D. Don shoots in vitro, and reported that maintaining ‘shoot hedge’ (shoot clumps maintained like mini-hedges in the same vessel for multiple production of shoots) in vitro contributed to rapid production of shoots. The simulated results in the present study generally agree with that observation in terms of enhanced production by using shoot hedges (or stock plant bases) as propagules. The integrated $D_f(t)$ for 100 d when both cuttings and stock plant bases were used as propagules was smaller ($5.47 \times 10^3$ and $3.68 \times 10^3$ with cuttings vs. $3.58 \times 10^3$ and $7.78 \times 10^3$ with cuttings and stock plant bases under LOW and HIGH conditions, respectively), and thus the ratio of integrated $D_f(t)$ to integrated $F_c(t)$ was smaller, than when only cuttings were used as propagules under the same environmental conditions. Those values should be small for minimizing waste of plant material. Reducing the percentage of plants that are propagated and later discarded is important for efficient operation of commercial nurseries (Hartmann et al., 1997). The present simulation suggested that use of stock plant bases in addition to cuttings saved energy and resources for growing stock plants by reducing plant waste. However, the PRDT(t) was smaller.

![Simulated numbers of harvested sweetpotato cuttings (Pc), cuttings leaving the system (Fc), stock plant bases to be discarded (Df) and total stock plants in the propagation area (TTL) with different alpha(t) values (ratio of number of cuttings to leave the system to that of cuttings harvested on day t. alpha(t) = 0.05, 0.2, 0.5, or 0.95, 0 ≤ t ≤ 100). Simulation in Scenario #1.](image-url)
than that for cuttings only. The PRDT (t) were constant for cuttings (5.6 and 10.4 under LOW and HIGH conditions, respectively), while variable for both cuttings and stock plant bases (0.4 to 5.6 and 0.3 to 10.4 under LOW and HIGH conditions, respectively). The PRDT (t) decreased when stock plant bases were used because many stock plants continued in the propagation system.

The HIGH conditions provided 7.1 and 12 times as great an integrated FC (t) for 100 d as did the LOW conditions with and without use of stock plant bases as propagules, respectively. Note that the impact of the environmental conditions was more pronounced when only cuttings were used as propagules. The HIGH conditions increased the integrated D_b(t) for 100 d, but decreased the ratio of integrated D_b(t) to integrated F_c(t) for 100 d. Values of PRDT (t) were higher under the HIGH than under the LOW conditions, since more cuttings were produced per stock plant. Controlling environment to enhance the multiplication rate, in combination with selecting a proper propagation method, could optimize the propagation process.

CONCLUSIONS

The generic models developed in the present study were effective tools for qualitative understanding of transplant production by vegetative propagation. Application of developed models to sweetpotato vegetative propagation has shown that they can be used for propagation planning and environmental control based on simulation and optimization. The simulations successfully predicted the effects of environmental conditions and propagation methods on numbers of each class of propagules and stock plants after many propagation cycles and were effective in analyzing production efficiency. Propagation can be optimized by selecting optimal combinations of production methods and environmental conditions based on simulations. Modified models will be applicable to other types of vegetative propagation and to other transplant production systems as well, including plug seedling production, where various stages of seedling plugs are maintained in production systems.

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