Short communication

A population viability analysis of serendipity berry (Dioscoreophyllum cumminsii) in a semi-deciduous forest in Nigeria

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ABSTRACT

The search for natural sweeteners has prompted intensive research on plants with sweetening properties. Dioscoreophyllum cumminsii (Stapf) Diels is a dioecious, semelparous annual liana found as a late successional, understorey species in West African semi-deciduous forests. The fruits and subterranean tubers are intensely sweet and are both edible. The sweetening substance in D. cumminsii is a protein (monellin), which is 3000 times as sweet as sugar. Unfortunately, it is one of the threatened plant species in the country because of massive habitat loss and fragmentation. Conservation is now needed as a salvage programme. Population size is a major determinant of extinction risk. This has prompted the application of growth and population dynamics models to viability analysis of wild species. The aim of population viability analysis (PVA) is to determine the minimum viable population size (MVP) or area (MVA) of a particular species. In this paper, MVP was estimated for D. cumminsii using genetic models. The models simulated minimum effective population size of 6040 individuals ha^{-1} in the ratio of 5032 males to 1008 females. This suggests that to retain evolutionary potential, D. cumminsii requires an effective population size of more than the 500–5000 range considered adequate for many other species.

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1. Introduction

1.1. Population viability analysis

About 189 plant species are currently threatened in Nigeria (IUCN, 2004). The list might not have been exhaustive as many species especially the wild ones are yet to be evaluated (Obioh and Isichei, in press). Many of the forest species are threatened principally due to habitat loss and fragmentation (Okafor, 1993; Ola-Adams and Onyeachusim, 1993). Thus, many plant species especially the rare ones are now restricted to small isolated populations. Small populations usually face a high risk of extinction either from deterministic or stochastic causes (Shaffer, 1981). Conservation is now needed as a salvage programme.

Ecological modelling is usually applied in forestry in order to overcome the limitations of field investigations, make long-term projections of forest dynamics and have better understanding of vital ecological processes (Bugmann et al., 1996). Porte and Bartelink (2002) reported that forests dynamics are mostly modelled using distribution models such as MASSIMO (Thürig et al., 2005), gap models like JABOWA, FORET, FORECE

(Bugmann et al., 1996) and distance-dependent tree models including TREEDYN developed by Professor Bossel and co-workers at the university of Kassel, Germany. Process-based models of all kinds rest on process-based assumptions while inventory-based or descriptive empirical forest models are based on statistical relations.

However, interest has grown in long-term population dynamics of wild species in response to human activities and the ability of certain key species to withstand environmental stresses, without the possibility of becoming extinct. This has prompted the application of growth and population dynamics models to viability analysis of wild species. The factors affecting extinction risk are ultimately manifested in the species (Lande, 1998) and population size is a major determinant of extinction risk (Reed et al., 2003). Consequently, conservation based on species and population dynamics has now become a feasible tool for determining extinction risks. The population viability analysis (PVA) approach has proved useful in this respect. Population viability analysis is the procedure that predicts the expected lifetime of a population. It is a process in which the likelihood that a population will become extinct is assessed, within a specified time and under particular circumstances (Shaffer, 1981; Possingham, 1991; Barbault and Sastrapradja, 1995). The process involves the use of numerical models to determine the minimum viable population size (MVP) or area (MVA) of a particular species. Although some researchers have started criticising the use of MVP in determining the PVA of organisms, no alternatives have been suggested yet (Reed et al., 2003). Minimum viable population size, which refers to the effective population size or the genetic neighbourhood size (N_e) is the population size that provides a given probability of persistence of a population for a given amount of time. Populations less than MVP are considered to be in imminent risk of extinction.

The MVP models are inventory-based, single species empirical models. When applied to plant species, they appear mostly related to the single-tree empirical models since both are species dependent and would use readily available input data to estimate forest development. However, while most single-tree empirical growth models predict basal area increment per hectare, the MVP models predict adult stem density per hectare needed for long-term survival.

Most estimates of MVP are based on genetic models because the theoretical models are either unrealistic or involve unresolved mathematical problems while the simulation models lack generality and require extensive data, many of which are not usually available (Shaffer, 1981). Unlike actual population size (N), MVP is difficult to ascertain and the situation is worse for plant populations due to lack of available evidence of N_e for them (Barrett and Kohn, 1991). Burgman et al. (1993) reported that the effective size of wild populations is usually substantially less than the actual size because of large variance in progeny numbers, unequal sex ratio among breeders and temporal fluctuations in population size. Theoretical and empirical evidence have shown that N_e is often between 10 and 50% of wild populations (Burgman et al., 1993; Frankham, 1995). Franklin (1980) suggested that inbreeding N_e should be 50 while that of variance should be 500. However, recent estimates recommend that variance N_e should be equal to 5000 (Lande, 1995).

Rapid, extreme environmental changes place a premium on genetic variability and adaptability of populations in fragmented habitats. For many species therefore, persistence will depend primarily on maintaining ample genetic variation for adaptive evolution (Lande, 1998). Thus, variance N_e may be of great importance in assessing vulnerability and adaptation of species to the current global change.

Several useful models for estimating variance N_e have been developed in recent years and reviewed by Burgman et al. (1993). Which model to use for a particular case should be dependent on the environmental and life history characteristic of the species. Particular attention should be paid to the species' biology and mating system and the assumptions that can be made concerning the species' reproductive behaviour. Lande and Barrowclough (1987) have derived numerous expressions for variance N_e to account for different mating systems and reproductive behaviour. Analyses of the models show that the size of a viable population is not static. Changing circumstances will alter the size and estimates of N_e will change as new information is found and is incorporated into the models. Models therefore, would not go far in analysing viability of populations unless there are adequate and reliable data in formats needed by each model. The aim of PVA is to determine the MVP or MVA of a particular species. In this paper, MVP was estimated for *Dioscoreophyllum cumminsii* using genetic models.

1.2. The species

Serendipity berry [*D. cumminsii* (Stapf) Diels] is a dioecious, semelparous annual liana found as a late successional, understorey species in West African semi-deciduous forests. The life cycle of *D. cumminsii* as summarised by Ahuama (2004) is presented in Fig. 1. The species has a complex life cycle. While the males propagate asexually by subterranean tubers, which might have impacted on the species genetic variability, the females reproduce sexually by seeds. The fruits and subterranean tubers are intensely sweet and are both edible. The sweetening substance in *D. cumminsii* is a protein (monellin), which is 3000 times as sweet as sugar (Holloway, 1977). The species therefore, has very high potential as a source of natural, non-carbohydrate sweetener.

2. Methodology

2.1. Floristic survey

Existing literature on Nigerian flora reveal that *D. cumminsii* is presently rare. However, a few of the forest reserves in Nigeria still have wild remnant populations of the species. The Biological Garden of Obafemi Awolowo University, Ile-Ife (7°30′–7°32′N and 4°31′–4°33.5′E) is one of such sites that was identified and used for this study. Permanent sample plots, 25 m × 25 m each were marked and laid out randomly in the Biological Garden in February 1998. Preliminary observations in 1997 showed that the tubers sprout at the onset of the early rains in March. Observation and data collection therefore started in March 1998. The life history, phenology and popu-
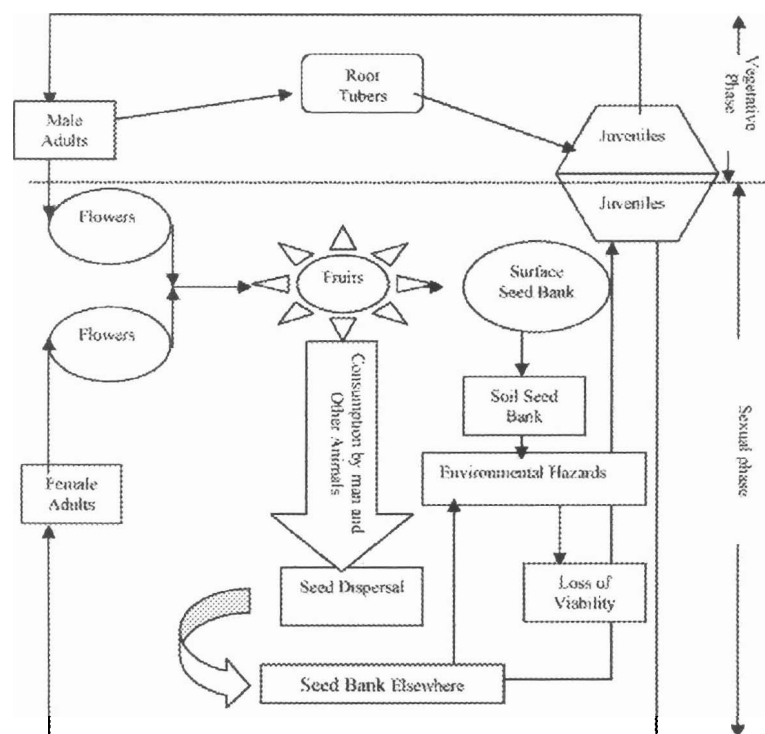
Fig. 1 – The life cycle of *Dioscoreophyllum cumminsii* (culled from Ahuama, 2004).

lation dynamics of *D. cumminsii* were monitored in these plots for 2 years.

Abundance data on the species were collected by random sampling method. Plot totals were computed. The densities of juveniles, non-reproducing adults and reproducing adults (males and females) as well as the total density for the species were estimated. From the data collected, the MVP for the species was estimated after two generations (years) following the genetic models of Lande and Barrowclough (1987) as described in Burgman et al. (1993).

2.2. The models

According to Lande and Barrowclough (1987), the genetic model for estimating the MVP per unit generational time in dioecious species with discrete generations and unequal sex ratio is given by

$$N_e = 4\left[\frac{1}{N_{em}} + \frac{1}{N_{ef}}\right]^{-1} = 4\left[\frac{N_{em}N_{ef}}{N_{em} + N_{ef}}\right], \quad \sigma^2 = \text{variance} \quad (1)$$

where N_e is the MVP for the species, N_{em} the effective size of males and N_{ef} that of females. If k represents the number of progeny produced by an individual during its lifetime, $\bar{k}$ and σ_k^2 are the mean and variance of k, respectively, for each sex, Lande and Barrowclough defined N_{em} and N_{ef} as

$$N_{em} = \frac{N_m \bar{k}_m - 1}{\bar{k}_m + (\sigma_{k_m}^2/\bar{k}_m) - 1} \quad (2)$$

and

$$N_{ef} = \frac{N_f \bar{k}_f - 1}{\bar{k}_f + (\sigma_{k_f}^2/\bar{k}_f) - 1} \quad (3)$$

From Eqs. (2) and (3), $\bar{k}$ and σ_k^2 for each sex is usually needed for the calculations of N_{em} and N_{ef}. However, it may be difficult in practice to determine these parameters in *D. cumminsii* populations in the wild because juveniles and non-reproducing adults of both sexes are indistinguishable. N_{em} and N_{ef} were thus assumed to be equal to N_m and N_f, respectively, where N_m and N_f are actual census numbers of reproducing (flowering) males and females in the population. For *D. cumminsii* therefore, the parameters N_m and N_f were determined and substituted for N_{em} and N_{ef} in Eq. (1) for each year. In 1999, N_m and N_f were 9125 and 1825, respectively, while in 2000 they were 8850 and 1800, respectively.

A long-term effective population size can be estimated by combining the effective numbers in different generations, $N_e(1), N_e(2), \ldots (N_e t)$ using the formula:

$$N_e = \frac{1}{2}\left[1 - \left\{\prod_{i=1}^{t}\left(1 - \frac{1}{2}N_e(i)\right)\right\}^{1/t}\right] \quad (4)$$

where t is the number of generations.

All population sizes vary and the effective size of a population depends on these variations in population size through time (Lande and Barrowclough, 1987; Burgman et al., 1993).

Eq. (4) therefore takes care of fluctuations in population size through time and gives a more appropriate estimate of MVP for such a species. These equations are based on the assumptions that the populations are panmictic and that there is no selection, migration or mutation.

3. Results and discussion

Results show that D. cumminsii exhibits differential light spectral requirement between the sexes. Males were found in forest gaps, sometimes completely exposed. In all such exposed populations, no females were found. The absence of females among exposed populations may be because light is observed, from laboratory experiments, to inhibit seed germination (Holloway, 1977; Ahuama, 2004). Females were therefore, found in deeper shade in the same forests as the males, most often, far away from the males (about 5–10 m away). Both sexes were observed to be gregarious. A disproportionate sex ratio of 5 males to 1 female was observed.

D. cumminsii has both unusual sex ratio and variability in progeny numbers. Earlier reports (Summerfield et al., 1977; Okoro, 1980) stated that the males are usually more abundant than females and that the female tubers are sterile. However, no specific sex ratios were provided in these reports. The dominance of males appears to be a reflection of their vegetative propagation strategy. It might equally be that the male to female ratio is influenced by light spectral composition (Summerfield et al., 1977) since seed germination occurs only in shaded environments (Ahuama, 2004). Burgman et al. (1993) reported that these abnormalities in sex ratio and reproductive success are expected to increase the MVP of the species, suggesting that even in managed, optimum populations, the species is likely to be threatened by these genetic factors.

Population densities of 10950 ha^{-1} (9125 males and 1825 females) and 10650 ha^{-1} (8850 males and 1800 females) were estimated for D. cumminsii in the first and second generations, respectively. The data were substituted in Eq. (1) to arrive at MVP of 6083 individuals ha^{-1} for the first and 5983 individuals ha^{-1} for the second generations. These values were used as inputs into the long-term effective population size model, Eq. (4). The model simulated a viable population size of 6040 individuals ha^{-1} for the species. This viable population is expected to contain 5032 males and 1008 females.

The implication of this result is that genetic drift would occur in the D. cumminsii population of 10800 at a rate equal to that expected in a population of 6040 randomly mating individuals. This is the minimum effective population size that is likely to maintain sufficient genetic variability for adaptation to changing environmental conditions (Shaffer, 1981). It is worth noting that this is not a rule of thumb but a guide to conservationists. Smaller population sizes disproportionately influence MVP (Begon et al., 1990) therefore; these values are expected to vary slightly when more generational data are used as inputs to the models (Reed et al., 2003). The estimates however, agree with Lande (1995) that Shaffer's MVP should not be less than 5000 and should actually be more in order to maintain disease resistance in populations. The MVP estimates from this study illustrate how inaccurate the generalized crude model ($N_e = N/1.4$ where N_e is the MVP and N

is the actual population size of reproducing adults (Burgman et al., 1993)) could be but supports the widely held view that MVP varies from 10 to 50% of extant populations or even more. The mean and variance ($\bar{k}$ and σ_k^2) of the progeny numbers of each sex could not be quantitatively estimated in this situation since the juveniles of both sexes are morphologically similar. This might have limited the precision of the projections. It might therefore be necessary for future developments of MVP models for forest plant species to contain a factor (which will depend mostly on the adult sex ratio and reproductive potential) that will correct N_m and N_f to N_{em} and N_{ef}, respectively, for each sex whenever juveniles of the two sexes are indistinguishable. This first calls for further studies that would establish the relationship between N_m and N_f and N_{em} and N_{ef}, respectively.

MVP models like every other model are built on assumptions, which may not be very realistic in nature but meant to simplify the model application. A generalised model or mechanical application of published models to other cases is likely to generate faulty conclusions (Soulé, 1987; Stork and Samways, 1995) since MVP is species- and site-specific. It is therefore obvious that every researcher should first determine the model to be used by adopting the most representative model for the species and adjusting the parameters based on the biology of the species. Our simulations have given insight into what the viable size of D. cumminsii should be but reliability could be enhanced by further studies that will provide more age-, sex-, species-specific and generational data.

4. Conclusion

This paper tried to estimate MVP for D. cumminsii using Lande and Barrowclough (1987) genetic models. The models simulated minimum effective population size of 6040 individuals ha^{-1} in the ratio of 5032 males to 1008 females. This suggests that to retain evolutionary potential, D. cumminsii requires an effective population size of more than the 500–5000 range considered adequate for many other species. The MVP estimate of 6040 individuals ha^{-1} for D. cumminsii may imply that genetic drift will occur in the species population at the rate equal to that expected in a population of 6040 randomly mating individuals. Populations lower than this and of different ratios are likely to be driven to extinction. However, the inability of the models to estimate the mean and variance of the progeny numbers of each sex in this situation might have limited the precision of the projections. It is suggested that future developments of MVP models for forest plant species should integrate a factor that will correct N_m and N_f to N_{em} and N_{ef}, respectively, for each sex whenever juveniles of both sexes appear indistinguishable.

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