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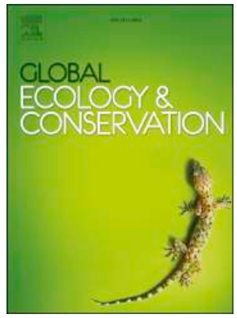

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PII: S2351-9894(19)30312-9

DOI: https://doi.org/10.1016/j.gecco.2019.e00807

Reference: GECCO 807

To appear in: *Global Ecology and Conservation*

Received Date: 14 June 2019

Revised Date: 3 October 2019

Accepted Date: 3 October 2019

Effect of Seasonality and Light Levels on Seed Germination of the Invasive Tree *Maesopsis eminii* in Amani Nature Forest Reserve, Tanzania

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Abstract

Studies on germination behavior are important tools for understanding how environmental factors affect geographic distribution and colonization of invasive plants. Particularly seedlings of invasive plant species benefit from high light intensity, as often found in disturbed areas of low canopy cover. We investigated the effect of various shade levels on seed germination and early growth of the invasive tree *Maesopsis eminii* at the nursery of a biodiversity hotspot, the Amani Nature Forest Reserve, Tanzania. Shade houses provided forest-like sun flecks of four categories (0%, 50%, 65% and 85% shade), representing light regimes found in tropical natural forests throughout the entire growing season. The average germination rate across the four different shade levels differed significantly during the dry season ($F_{3,12}$ = 48.74, P<0.001) but not in the wet season ($F_{3,12}$ = 3.49 , P = 0.051). Final germination percentage at 0% shade was 1.5 times higher compared to that under 85% shade during the wet season. In both dry and wet seasons, stem diameter, shoot height, total fresh and dry biomass significantly decreased with an increase in shade levels. During the dry season, leaf chlorophyll contents were three times higher at 85% and 65% shade than at 0% shade. Both seasonality and shade levels as well as their interactions influenced most germination parameters but not growth parameters except stem diameter. The conclude that *M. eminii* seed germination is fostered by light as it prefers colonizing in forest gaps, and lower light levels might act as a barrier to its invasive capacity, particularly during the dry season. Hence, management strategies of *M. eminii* should include the provision of unfavorable light regimes and take seasonality into account.

Keywords: *Shade, Biodiversity hotspot, Tree seedling, Forest gaps, Disturbance*

1. Introduction

Biological invasion is the introduction and establishment of an invasive species beyond its natural range, where it may proliferate and spread dramatically (Simberloff, 2013). The International Union for Conservation of Nature (IUCN) defines invasive plant species as those plants established in natural or semi-natural ecosystems or habitat, become an agent of change, and threaten native biological diversity (IUCN, 2000). Biological invasions caused by invasive plant species is one of the major threats to biological diversity reported by scientists and one of the main factors driving environmental degradation in various parts of the world (Nottingham et al. 2019). Invasive plant species become well established, transform and dominate the ecology of their adoptive homes by suppressing or displacing resident species or by subverting and disrupting the functional integrity and service delivery of colonized ecosystems (Boy, 2005). Once established, invasive plant species can spread rapidly, impoverishing biodiversity and undermining human welfare, while damaging native species, ecosystems and communities as well as causing loss and degradation of habitats (Viisteensaari et al. 2000).

Forest ecosystem and rangelands have been increasingly infested by both woody and herbaceous invasive plants (Binggeli, 1998). Some of these invasive plant species can have cascading impacts such as alteration of tree species composition, changes in forest succession, declines in biological diversity, and alteration of nutrient, carbon and water cycles (Liebhold et al. 2017). In India, *Leucaena leucocephala*, which was planted as a fodder crop in agroforestry systems due to its prolific natural regeneration in open gaps, quickly became a problematic invasive tree species (Binggeli, 1998). In Ethiopia and Kenya, *Prosopis juliflora* is one of the world's worst woody invasive plant forming impenetrable shrubby thickets, causing an irreversible displacement of beneficial native species, pasture grasses as well as native tree species (Abdulahi et al. 2017; and Obiri, 2011).

In natural habitats, successful invasion and colonization ability of invasive plant species are influenced by both biological and environmental factors (Moghadam and Alaei, 2014). Invasive plant species' seed germination, seedling establishment and geographical distribution are affected by a wide range of environmental factors such as light intensity, temperature, water availability, soil salinity, seasonality (dry and wet), functional traits and others (Dibenedetto, 1991; Flores et al., 2016; Maharjan et al., 2011). Therefore, invasive species with prolific seed production and dispersal mechanisms find favorable environmental factors in new habitats and can spread faster (Green et al. 2004). Seed germination has been stated as one of the most critical stages in the natural regeneration of invasive plant species. The process is influenced by light intensity, temperature and moisture content (Zhang et al. 2012). Therefore, studying seed traits and germination behavior is an important step towards developing guidelines and strategies for prevention and control of invasive plant species.

The response of seeds to light during germination is an important development phase, playing a critical role in seedling establishment and overall environmental adaptation for invasive plants (Fenner and Thompson, 2005). A study by Leal et al. (2013) indicated that the invasive species *Cortaderia jubata* has three times higher germinability under high light than in dark conditions. Survival, growth and death of *M. eminii* seedlings were investigated under contrasting environments where by a higher germination percentage of up to 92% was found in open environment and a lower survival rate of *M. eminii* seedlings were found in the shaded environment (Binggeli, 1989). Despite all these studies on the success of invasive plants, light sensitivity and performances of *M. eminii* seeds under different shade levels during germination stage has never been quantified and, up to now there has been no experimental approach conducted to establish the optimal light level for *M. eminii* seed germination across different seasons. As many alien plants show an increase in their germination rates when exposed to high light conditions this study provides potential invasion hotspots and will help management to limit invasion ability and colonization of new forest habitats.

In addition, variation in seasonality has also shown to have an influence on germination success and spread, particularly for invasive plants that lack vegetative propagation (Fenner and Thompson, 2005). To understand factors for invasiveness and devise sustainable management of invasive tree species particularly *M. eminii*, detailed knowledge of its seed ecology is crucial for understanding its invasive behavior. Kyereh et al. (1999); Leal et al. (2013); and Svriz et al. (2014) indicated that studies on germination behavior in response to light levels are useful tools in the investigation of environmental factors affecting geographic distribution as well as for understanding colonization abilities and adaptation strategy of exotic plants introduced in new habitats. In this paper, we hypothesized that the rate of germination of *M. eminii* seeds will decrease with the increase in shade levels. We further hypothesized that wet season conditions would be more favorable for *M. eminii* seedling establishment than the dry season. To test for these hypotheses, we quantified both *M. eminii* seed germination and growth parameters in experiments at the Amani Nature Reserve nursery, Tanzania. Germination parameters included five parameters which are the Final Germination Percentage (FGP), Mean Germination Time (MGT), Germination Index (GI), Coefficient of Velocity of Germination (CVG) and Germination Rate Index (GRI). Also, the study evaluated morphological growth characteristics of germinated *M. eminii* seeds in order to establish variation in seedling health and quality. Growth parameters evaluated during this study included the shoot height (SH), stem diameter (SD), total fresh biomass (TFB), total dry biomass (TDB) and total leaf chlorophyll content (ChC).

1.1 Botanical description of *Maesopsis eminii*

Maesopsis eminii (Rhamnaceae family) is an angiosperm drought-tolerant rain forest tree (Epila et al., 2017a). The species has simple alternate leaves with an obovoid drupe fruit 20-35 x 10-18 mm, changing from green to yellow to purple-black when mature (Orwa et al., 2009). According to Mugasha, (1981) *M. eminii* trees possess flowers that are bisexual and yellowish-green. It is a fast growing, gregarious pioneer and semi-deciduous tree, which can reach up 10 - 30 m in height with a clear bole up to 20 m and 70 - 80cm diameter at breast height (Viisteensaari et al., 2000). The species germinates successfully and grows well in disturbed areas with canopy gaps of at least 300 square meters (Kilawe et al. 2018). Similarly, Cordeiro et al. (2004) found that the greatest proportion of experimental seeds of *M. eminii* germinated in large tree-fall gaps and forest edges, where light and availability of bare humus soil enhanced germination process. It is extremely competitive in forest gaps and secondary forests, survive well on poor soils and have a faster growth rate than coniferous trees, which has accounted for its extensive use in afforestation enrichment, ecological restoration, plantation forestry and agroforestry practices (Ani and Aminah, 2006; Orwa et al., 2009).

In the East Usambara Mountains, *M. eminii* was used for afforestation enrichment and restoration to fill forest gaps and clear-felled areas after expansion of peasant's agriculture and large scale logging operations in the 1960's (Geddes, 1998; Hall, 1995). Binggeli (1989) reported that preference of *M. eminii* was due to its quick growth rate and a 40-years felling cycle instead of 80-years for other native trees producing hard wood. In other parts of Tanzania, the species is widely used in home gardens as shade or border tree and for timber production due to its rapid regeneration (Hall, 2010). Outside Tanzania, *M. eminii* has been extensively used across the tropics in timber plantations and as a key component in agroforestry (Hall, 2010). Reports indicate the use of *M. eminii* as a shade tree in coffee, banana, cocoa and cardamom plantations in Kenya, India, Congo, Uganda, Indonesia and in Ghana (Hall, 2010).

Invasion of *Maesopsis eminii* in East Usambara

Maesopsis eminii is typically a Guineo-Congolian species, with its range corresponding to African lowland rain forest zone (Binggeli, 1989; Epila et al. 2017; Hall, 1995). In Tanzania, *Maesopsis eminii* has been found to be one of the highly successful invasive woody plants in Amani Nature Forest Reserve (Binggeli 1989; Binggeli and Hamilton 1993; Hulme et al. 2013). Binggeli and Hamilton (1993) presumed that this aggressive tree species were introduced to the East Usambara Mountain by Germans around the 1910s for plant experimental growth studies and to shade seedlings of native plants species such as *Cephalosphaela usambarensis, Newtonia buchananii and Berchemedia kweo* in order to enhance growth. Large scale planting in the 1960s and 1970s to fill logged forest gaps created a massive seed source of *M. eminii* and helped this species spread into the endemic rich natural forests due to its fast growth rate and prolific seed production (Hall, 1995; Hamilton and Bensted-Smith, 1989). This invasive tree is becoming a dominant species in natural forestry as well as agroforestry systems in the East Usambara Mountains, Northern Tanzania (Hall et al., 2011), and its dominance leads to impoverished understory scrub and herb vegetation and alternated canopy structure and species composition (Musila, 2006). However, not much is known on the factors contributing to its invasive success and susceptible areas, which must be identified to inform sustainable management options.

Apart from the East Usambara mountains, *M. eminii* invasion has also been reported on Pemba island, Tanzania, and in Puerto Rico (Hall, 2010). Various ecophysiological studies have been conducted to shed light on the aggressive nature of *M. eminii*. Epila et al., (2017b) and Hubeau et al., (2019) demonstrated that adaptive physiological responses such as an active phloem loading strategy and drought-induced cavitation proved to be successful for its colonization. Hydraulic capacitance linked to anatomy and leaf-water relocation seems to be one of the crucial ecophysiological traits for the drought-resistance of *M. eminii* (Epila et al., (2017b). These unique characteristics, in addition to drought-deciduous leaves, the ability to tolerate drought for up to 6 months, its fast growth capability and high light demand promote this species' invasive nature (Eggeling, 1947; Epila et al., 2017b, 2018; Hubeau et al., 2019). However, there is no clear information on whether these attributes are also valid for *M. eminii* invasion in East Usambara, Pemba and Puerto Rico islands. This study focuses to assess seed biology (germination) in response to light levels and seasonality as one of the physiological traits of *M. eminii* in relation to its invasiveness. We assessed germination of *M. eminii* seeds in both wet and dry seasons using germination parameters, namely Final Germination Percentage, Mean Germination Time, Germination Index, Coefficient of Velocity of Germination and Germination Rate Index (GRI) similar to Ajmal Khan and Ungar, (1998) and Al-Ansari and Ksiksi (2016). We also evaluated growth parameters (shoot height, stem diameter, total fresh biomass, total dry biomass and total leaf chlorophyll content) to assess seedling health across different shading levels and seasons.

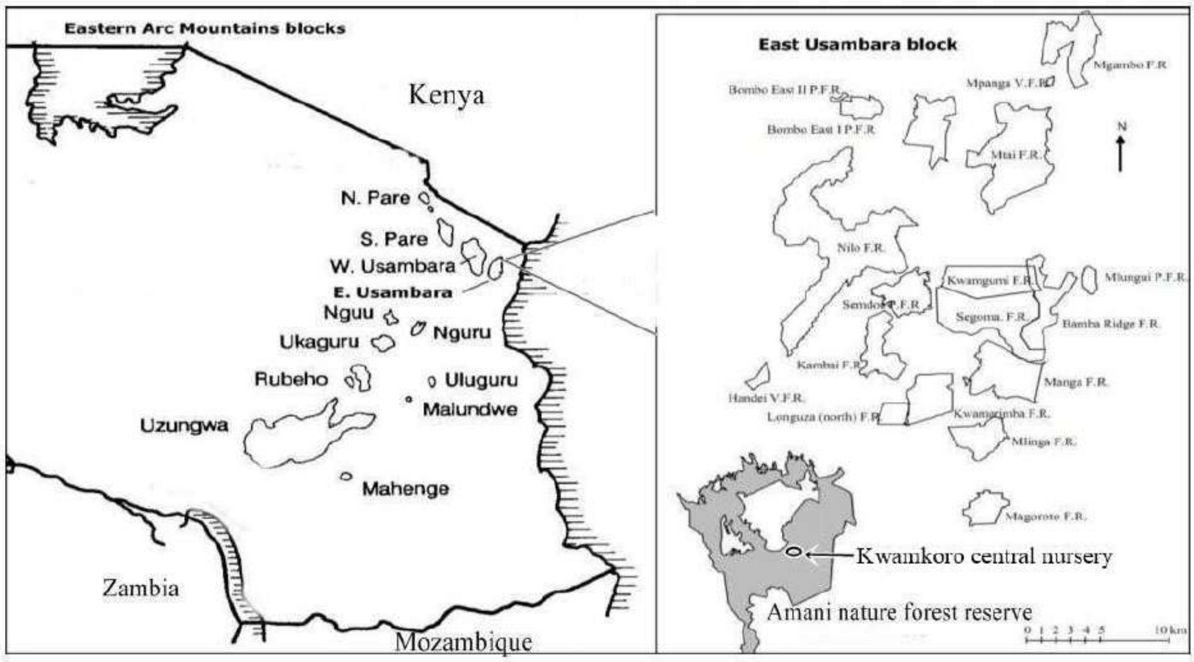
2. Materials and methods

2.1 Study area

The study was conducted in Amani Nature Forest Reserve (ANFR) at Kwamkoro Central Nursery. The reserve is located at 5°5'S and 38°40'E, at 950 masl, in North Eastern Tanzania (Figure.1). The reserve is with 8,360 hectares, the largest nature reserve in the East Usambara Mountains and renowned for its high biodiversity per unit area (Miller, 2013). According to Frontier Tanzania (2001) and Hulme et al. (2013), the reserve is home to seven endangered and 26 vulnerable species according to IUCN categories, while six animal species and one sub species are considered endemic to the Usambara Mountains. Recently, invasion by exotic *M. eminii* was noted to be a serious threat to the Amani Nature Forest Reserve (Gereau et al. 2016). Casual observations indicate that the species has reached nearby forests such as Mlinga, Magoroto and Nilo Forest Reserve. In the late 1980s, 15% of gaps in Amani nature reserve contained *M. eminii*, with floristically impoverished understory vegetation, little regeneration of primary forest trees and poor animal and plant diversity including that of the soil fauna (Hamilton and Bensted-Smith, 1989). Invasion and spread of *Maesopsis* in Amani have raised concerns that it may dominate a significant area of the forest and thereby negatively impacting the biodiversity (Hall et al. 2011).

Figure 1:

Map of East Usambara showing the location of Amani Nature Forest Reserve and Amani central nursery.



2.2 Study design

The experiment was conducted in shade houses at the central nursery, Kwamkoro Station, in Amani Nature Forest Reserve. Shade houses (Fig 2) were constructed with shade net (hessian nylon, Illuminum Company Ltd, Nairobi Kenya) to provide forest-like sun flecks. Shade nets (one meter squire each side) were calibrated with shade level-categories of 0% (L0), 50% (L50), 65% (L65) and 85% (L85), representing light regimes frequently found in tropical natural forests throughout the entire growing seasons (Flores et al. 2016; Kyereh et al. 1999; Svriz et al., 2014). We adopted methods for seed germination experiments in *Pinus* species by Zhang et al., (2012) with some modification. *Maesopsis eminii* seeds were obtained from Amani Central Nursery, collected in February 2018 and air dried for four weeks before sowing as recommended by in Hamilton and Bensted-Smith (1989).

Figure 2
Shade houses for *Maesopsis eminii* seed germination experiments at Kwamkoro central nursery, Amani Forest, Tanzania. Shade house A = 50% shade level, B = 65% shade level C= 85% shade level.

Soils were collected from the forest, sieved to exclude residual roots or seeds and air dried prior to use. Ten seeds were sowed per each shade category and replicated four times, i.e., a total of 160 seeds were sowed. Seed beds at each shade level were kept moist by regular watering *ad libitum*. In this experiment, germination was defined as the first needle or radicle sprout becoming visible (Flores et al. 2016) and germination success was recorded at 7-day intervals and ceased when no further seeds germinated for more than one week. The experiments were carried out in March and April, 2018, during the wet season, with an average monthly precipitation and temperature of 256 mm and 23^{o}C and repeated during the dry season, in July and August, 2018, with average precipitation and temperature of 67 mm and 15^{o}C, respectively (Frontier Tanzania, 2001; Hall et al. 2011).

2.3 Data collection and analysis

2.3.1 Germination parameters

Five different germination parameters namely Final Germination Percentage (FGP), Mean Germination Time (MGT), Germination Index (GI), Coefficient of Velocity of Germination (CVG) and Germination Rate Index (GRI) were assessed consistently to (Ajmal Khan and Ungar, 1998; Al-Ansari and Ksiksi, 2016; Aravind et al. 2018; and Kader, 2005). Final Germination Percentage (FGP) attained under each shade level was calculated as:

(1) $FGP = \frac{Ng}{Nt} x100\%$

Whereby N_g = Total number of seeds germinated and N_t = Total number of seeds evaluated. The Mean Germination Time (MGT) of seeds under a given shade level was calculated as:

(2) $MGT = (\sum Ni * Ti)/(\sum Ni)$

Whereby N_i = Number of seeds germinated per day and T_i = Number of days from the starting the experiment. The FGP and MGT were combined and presented in the form of Germination Index (GI) calculated based on the formula:

(3) $GI = \sum Nx * Ti$

with N_x = Number of germinated seeds at the end of the experiment and T_i = Number of days from the beginning to the end of the experiment. Coefficient of Velocity of Germination (*CVG*) was calculated to find out the rapidity of germination through the following formula:

(4) $CVG = (\sum Ni * 100)/(\sum Ni * Ti)$

Ni = Number of seeds germinated in a given period of time, *Ti* = Number of days, Germination Rate Index (*GRI*) represented the percentage of germination per day and was calculated by the following formula:

(5) $GRI = \sum\ Ni/Ti$

Where *Ni* = Number of seeds germinated in a given time, *Ti* = Number of days.

2.3.2 Growth parameters

We measured shoot height (SH), stem diameter (SD), total fresh biomass (TFB), total dry biomass (TDB) and total leaf chlorophyll content (ChC) as morphological indicators of seedling health and quality (Haase, 2008) across various shade level treatments during dry and wet seasons. We selected five *M. eminii* seedlings from each replicated site and measured shoot height using a meter stick. This was measured as a vertical distance from the cotyledon scar to the end of the growing tip similar to (Mexal et al. 1990). Stem diameter was measured with digital calipers perpendicular to the stem at the scar of first leaf as an average of five seedlings in each replicate. Total fresh and dry (dried at 65^{o}C for 48 hours in hot air Asian oven manufactured by IndiaMART, New Delhi) biomass was recorded using a digital weighing scale and represented shoot and root mass of *M. eminii* seedlings (Haase, 2008; Mašková and Herben, 2018).

Leaf chlorophyll content (ChC) of *M. eminii* seedlings from each shade level were extracted based on procedures similar to Alpert (1984) and Ngondya et al. (2016). We picked leaves from five seedlings selected randomly from replicates in each treatment. 70 mg of young fresh leaves were immersed in 6 ml of Dimethyl Sulfoxide (DMSO) without grinding, and incubated at 65°C for 12 h in Asian oven manufactured by IndiaMART, New Delhi. The extract was transferred to a test tube and made up to a total volume of 10 ml with more DMSO. A 3 ml chlorophyll extract of *M. eminii* leaves were transferred into glass cuvettes to determine optical density (OD) of the sample. The OD of blank liquid (DMSO) and that of *M. eminii* samples were determined under 2800 UV/VIS spectrophotometer (UNICO®) at 663 nm and 645 nm based on (Hiscox and Israelstam, 1979). The absorbance of the blank was deducted from the absorbance readings of every sample prior to calculations being made. *M. eminii* leaf chlorophyll contents were calculated based on the equation: $Leaf\ Chlorophyll\ content = 0.0202A663 + 0.00802A645$ (Hiscox and Israelstam, 1979); where A663 and A645 are absorbance readings at 663 nm and 645 nm, respectively.

Before analysis, all data were tested for normality using Shapiro Wilks test where results greater than 0.05 were regarded as being normal distributed and those below data were considered to significantly deviate from normality. Effects of different shade levels and seasonality and their interaction on seed germination rates were compared using one-way ANOVA in a factorial design using Tukey HSD post hoc test. Level of significance was set at α = 0.05. Statistical analysis was carried out in version 20 IBM SPSS and OriginPro 2015 software.

3. Results

3.1 Germination during the wet and dry season

During the wet season, the mean number of germinated *M. eminii* seeds did not differ significantly across shade levels ($F_{3,\ 12} = 3.49$, P = 0.051; Table 1). However, there was a significant trend of the Final Germination Percentage (FGP) being 1.5 times higher at 0% shade level (L0) than that of 85% shade level (L85) and the Germination Index (GI) of L0 was twice as high compared to L85 (Table 1). Cumulative mean germination rate (Figure 4) was highest at L0 and lowest at L85. In general, all germination parameters declined slightly as shade levels increased (Table 1).

Figure 3
Germination for *M. eminii* seeds in Amani central nursery, Tanzania, in the seventh week of the experiment in 2019. Image A = 0% shade level, B= 50% shade level, C = 65% and D = 85% shade level. For germination rates over time, see Table 1 and Figure 4.

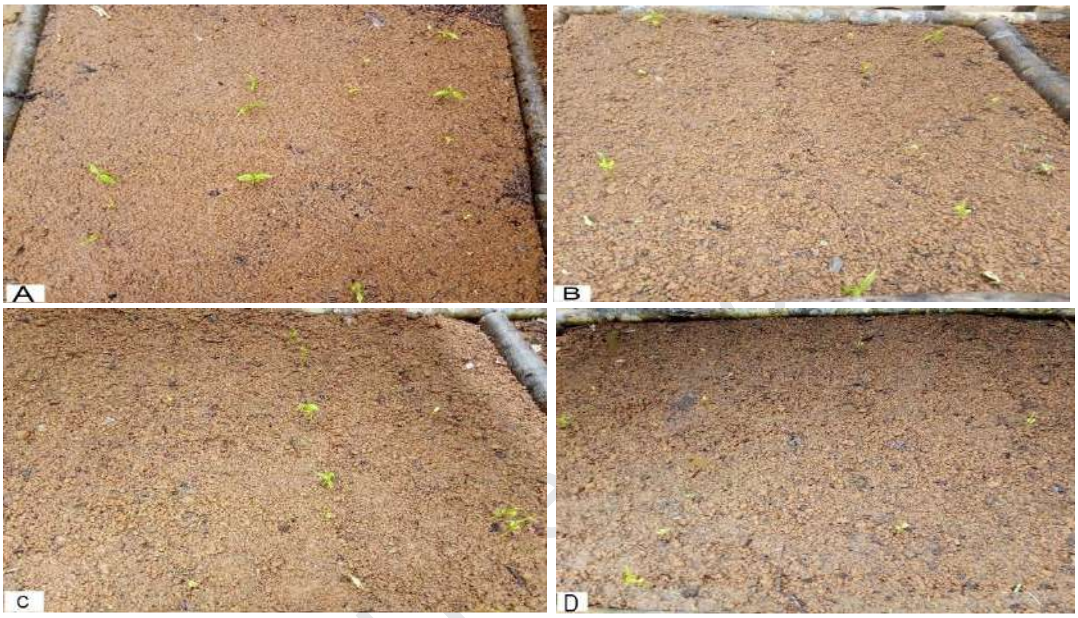
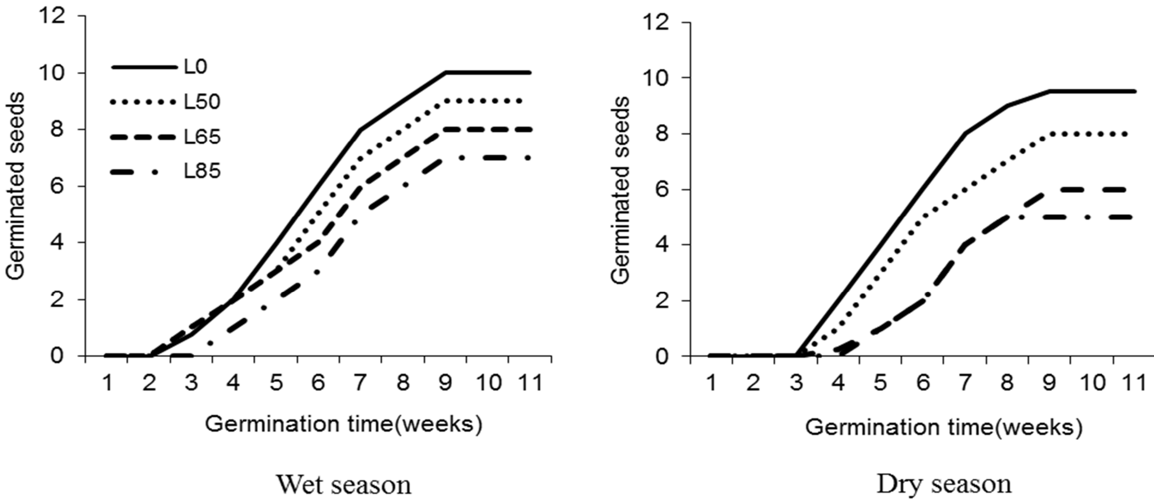


Table 1
One-way ANOVA test for germination parameters (± SE) during the wet and dry season after 12 weeks of germination experiment

Germination parameters	Season	L0	L50	L65	L85	$F_{(3,12)}$	P
Mean Germination Rate	Wet	9±0.3^{a}	8±0.4^{a}	9±1.0^{a}	7±0.5^{a}	3.49	0.051
	Dry	9.5± 0.6^{a}	7.5± 1.3^{a}	3.7± 1.3^{b}	1.3± 1.0^{c}	48.74	<0.001
Final Germination Percentage	Wet	93±1.7^{a}	88±1.8^{b}	78±1.8^{c}	55±1.6^{d}	146.05	<0.001
	Dry	95± 2.0^{a}	75± 2.0^{b}	38± 2.0^{c}	13± 1.0^{d}	589.68	<0.001
Mean Germination Time	Wet	38±1.5^{b}	43±1.5^{a,}	41±1.5^{a,b}	42±2.1^{a,c}	7.07	0.005
	Dry	39± 2.1^{a}	41± 2.1^{a,b}	44± 0.6^{b,c}	45± 1.0^{c}	14.46	<0.001
Germination Index	Dry	494±1.5^{d}	387±2.1^{b}	430±2.0^{c}	270±21^{d}	335.93	<0.001
	Wet	495± 1.0^{a}	313± 1.0^{b}	176± 1.5^{c}	58± 3.0^{d}	921.56	<0.001
Coefficient of Velocity of Germination	Dry	2.7±0.2^{a}	2.3±0.2^{b,d}	2.4±0.1^{b,c}	2.4±0.1^{c,d}	6.06	0.009
	Wet	2.6± 0.3^{a}	2.0± 0.4^{a}	2.3± 0.2^{a}	2.2± 0.4^{a}	2.69	0.093
Germination Rate Index	Dry	0.3±0.1^{a}	0.2±0.1^{a}	0.2±0.1^{a}	0.2±0.1^{a}	1.24	0.337
	Wet	0.3± 0.2^{a}	0.2± 0.1^{a}	0.1± 0.1^{a}	0.1± 0.1^{a}	2.44	0.115

Data in the same row with different letters represent significant differences between shade levels ($P < 0.05$) according to Tukey's Post Hoc test. Shade levels: L0 = 0% shade, L50 = 50% shade, L65 = 65% shade and L85 = 85% shade

Figure 4:
Germination time and cumulative mean number of *Maesopsis eminii* seeds that germinated during the wet and dry season over the period of 12 weeks. Line types reflect different levels of shade treatment: L0 = 0% shade level, L50 = 50% shade, L65 = 65% shade, and L85 = 85% shade.



Growth parameters of *Maesopsis eminii* seedlings during the wet season indicated significant differences, particularly in stem diameter, shoot height, total fresh biomass and chlorophyll content but not in total dry biomass across different shade levels (Table 2).

Table 2:
Mean growth parameters of *Maesopsis eminii* seedlings growing at different shade levels during the wet and dry season. Measurements were taken on the twelfth week of the experiment. L0 = 0% shade level, L50 = 50% shade, L65 = 65% shade, and L85 = 85% shade.

Growth parameters	**Season**	**L0**	**L50**	**L65**	**L85**	**$F_{(3,12)}$**	**P**
Stem Diameter	Wet	$2.57±0.1^{a}$	$2.68±0.1^{a}$	$1.98±0.1^{b}$	$2.48±0.1^{b}$	9.91	<0.001
	Dry	$2.3± 0.1^{a}$	$2.5 ± 0.1^{a}$	$1.9 ± 0.1^{b,c}$	$1.92 ± 0.1^{c}$	24.40	<0.001
Shoot Height	Wet	$13.2±0.2^{a}$	$19.1±0.5^{b,d}$	$20.4±0.9^{c}$	$17.7±0.7^{d}$	25.72	0.002
	Dry	$13.0 ±0.2^{a}$	$18.6 ± 0.6^{b,d,e}$	$19.3 ± 1.0^{c}$	$16.1 ± 0.5^{e}$	19.90	<0.001
Total Fresh Biomass	Wet	$4.9±0.1^{a}$	$8.4±0.5^{b}$	$9.0±0.2^{b}$	$5.9±0.5^{c}$	88.23	<0.001
	Dry	$3.9± 0.3^{a}$	$7.6 ± 0.4^{b,c}$	$8.6 ± 0.2^{c}$	$5.1 ± 0.3^{a}$	32.00	<0.001
Total Dry Biomass	Wet	$1.5±0.3^{a}$	$1.9±0.1^{a}$	$1.9±0.1^{a}$	$1.5±0.2^{a}$	3.42	0.054
	Dry	$0.9 ± 0.1^{a}$	$1.4 ± 0.1^{b,c}$	$1.4 ± 0.1^{c}$	$1.0 ± 0.1^{a}$	18.10	<0.001
Chlorophyll Content	Wet	$0.02±0.002^{a}$	$0.03±0.001^{b}$	$0.03±0.001^{b}$	$0.03±0.001^{b}$	15.9	0.002
	Dry	$0.01±0.001^{a}$	$0.02±0.001^{b}$	$0.03±0.001^{c}$	$0.03±0.001^{c}$	35.30	<0.001

Different letters across rows represent significant differences according to Tukey's Post Hoc ($P < 0.05$).

During the dry season, the mean number of germinated *M. eminii* seeds differed significantly across all shade levels. Tukey HSD test indicated that particularly at higher shade levels (65% and 80%), the germination rates were less than 30% of that 0%. Final Germination Percentage and Germination Index at 0% were both eight times higher than at 85% and GRI was three times higher as compared to that at 85% (Table 1). Furthermore, it took six days more (MGT) for *M. eminii* seeds to germinate in 85% shade as compared to germination time in 0% shade. In the dry season, all measured growth parameters (stem diameter, shoot height, total fresh and dry biomass as well as chlorophyll content) differed significantly with shade levels (Table 2). Stem diameter decreased with increase in the shade level, while ChC increased with increase in shade. At L85, ChC of *M. eminii* seedlings was three times higher than ChC in L0 shade level. SH, TFB and TDB increased with increase in shade levels at 50% and 65% but they were reduced at 85% shade level.

Figure 5

Prolific germination of *Maesopsis eminii* seeds on the forest floor beneath the mother tree in a forest gap (A) and *Maesopsis eminii* sapling thriving in an open forest gap (B) in Amani Nature Forest Reserve, Tanzania, in 2019.

3.2 Effect of seasonality on germination and growth parameters

We assessed the influence of both seasonality and shade level on germination and growth parameters of *M. eminii* seeds. All germination parameters were significantly reduced during the dry season expect for GRI and CVG. MGR and FGP were twice as high in wet season as compared to the dry season while FGP was three times as high in the wet than in the dry season. The main effect for shade level was significant at all germination parameters except for GRI. Similarly, the interaction effect was significant to all germination parameters except CVG and GRI (Table 3).

Table 3
Factorial ANOVA to compare main effects of seasonality (dry and wet), shade levels (0%, 50%, 65% and 85%) and the interaction between seasonality and shade level on the mean germination parameters of *Maesopsis eminii* seeds after 12 weeks.

Germination parameters	**Seasonality**		**Shade level**		**Interaction**	
	$F_{(1,24)}$	***P***	$F_{(3,24)}$	***P***	$F_{(3,24)}$	***P***
Mean Germination Rate	48.96	<0.001	35.91	<0.001	18.52	<0.001
Final Germination Percentage	536.64	<0.001	610.62	<0.001	161.34	<0.001
Mean Germination Time	5.36	0.029	15.51	<0.001	5.52	0.005
Germination Index	4913.61	<0.001	5044.37	<0.001	959.42	<0.001
Coefficient of Velocity of Germination	3.56	0.072	5.99	0.004	0.49	0.692
Germination Rate Index	1.11	0.304	3.43	0.033	0.45	0.720

We found that all growth parameters i.e., stem diameter, shoot height, total fresh biomass, total dry biomass as well as total chlorophyll content were significantly inhibited during the dry season as compared to the wet season. For example, total chlorophyll content and dry biomass were twice as high during the wet season as compared to during the dry season and decreased with an increase in shade levels. The main effect of shade was significant for all growth parameters while there was no significant interaction effect of the two variables except for stem diameter (Table 4)

Table 4
Factorial ANOVA comparing main effects of seasonality (dry and wet) and shading levels (0%, 50%, 65% and 85%) and the interaction effect between seasonality and shading level on mean growth parameters of *Maesopsis eminii* seeds after 12 weeks.

Germination parameters	**Seasonality**		**Shade level**		**Interaction**	
	$F_{(1,24)}$	***P***	$F_{(3,24)}$	***P***	$F_{(3,24)}$	***P***
Stem Diameter	26.09	<0.001	23.76	<0.001	3.31	<0.001
Shoot Height	7.33	0.012	32.39	<0.001	0.98	0.419
Total Fresh Biomass	7.98	0.009	103.53	<0.001	0.48	0.694
Total Dry Biomass	60.63	<0.001	12.61	<0.001	0.09	0.963
Total Chlorophyll content	43.77	<0.001	47.72	<0.001	1.94	0.150

4. Discussion

Seed germination and seedling establishment of invasive species in natural forest ecosystems are affected by environmental factors such as light, temperature, seasons and water availability (Leal et al., 2013). In this study, shade levels significantly influenced seed germination during the dry but not during the wet season. Similar to our findings, other studies such as Binggeli et al. (1993); Ioana et al. (2015) and Vieira et al. (2010) have found that invasive plants perform poorly in low light environments while displaying high survivorship and growth rate under high light conditions. Our findings of reduced germination during increase of shading level indicate that *M. eminii* seeds exhibit positive photoblastism, i.e. photoblastic seeds are capable of detecting light quality and quantity, a physiological process mediated by protein molecules referred to as phytochromes (Fenner and Thompson, 2005). These photoreceptors have a multiplicity of roles in plant physiology and have been the subject of plant invasion success and colonization abilities particularly during germination stage (Gioria and Pyšek, 2017). Our study found that optimal *M. eminii* seed germination occurs when exposed to 0% shade level during the dry season.

In our experiment, most (95% Final Germination Percentage) *M. eminii* seeds germinated after 38 days while seeds at >50% shade level took longer to germinate as compared to 0%. These average times taken for breaking *M. eminii* seed dormancy and activating germination process is similar to Binggeli (1989) who reported same germination period for freely fallen fleshy *M. eminii* fruits. Dawson et al. (2008) and Epila et al. (2017) also found that *M. eminii* seed populations showed high germination rates particularly in large forest canopy gaps and forest edges as long as soil moisture is sufficient and arboreal seed dispersers are present.

The Germination Index (GI) we calculated combined both percentage and speed of germination and it magnified the variation among seed lots with an easily compared numerical measurement (Kader, 2005). The high GI we recorded in 0% shade indicated a high germination arithmetic weight, which emphasizes the difference more clearly between germination percentage and speed along different shade levels. During the dry season we recorded a GI at 0% that was 737 units larger than at L50. Similarly, Leal et al (2013), observed that many alien plants show an increase in their germination rates when exposed to high light conditions, which favors their performance in disturbed areas. Vieira et al.

(2010) observed that seeds of an invasive weed, *Cortaderia jubata*, had three times higher germination success at high light conditions than in the dark in coastal California.

Further, we found that morphological growth characteristics and total chlorophyll contents were similarly influenced by shading level in both dry and wet seasons. According to Haase, (2008) and Qi et al. (2019) seedling morphology such as stem diameter, shoot height and total biomass allocation are characteristics most commonly examined in forest seedling stock to evaluate seedling quality. In this study, we found that most morphological characteristics of *M. eminii* seedlings were influenced by shade particularly during wet season. A large stem diameter predicted the best growth and survivorship of *M. eminii* seedlings in the 0 – 50% shade range. This large stem diameter is correlated with larger root systems and larger stem volume (Haase, 2008).

Similarly, shoots were taller in 0%-65% shade levels than under high shade, often associated with generally higher number of leaves and more access to sunlight enhancing photosynthetic capacity and transpiration, which is a competitive advantage over other species (Haase, 2008; Ranal and Santana, 2006; Udo et al. 2016). There seemed to be an optimal shade level range for *M. eminii* seedling growth between 0-65% shade, which is supported by findings of Binggeli (1989) who reported higher seedling survivorship and lower mortality rate of *M. eminii* seedlings in open environments as compared to shaded in southern Uganda. Total chlorophyll content followed a similar trend with a maximum value recorded at 65% shade, agreeing with Galicia-Jiménez et al. (2001) who found higher chlorophyll content in *Hopea helfery* and *Hopea odorata* under conditions of low light intensities at 58%, 78%, 92% shade level. This mechanism is explained by Dibenedetto (1991) and Niinemets et al. (1998) as a response used by the plants to optimize quantum harvesting when shading level increases.

Our study highlights the importance of adequate light levels in germination processes and hence, recruitment, establishment and distribution of *M. eminii* in the Amani Nature Forest Reserve. During the dry season particularly in the study area tall trees grow only little and lose a large number of their leaves, thereby increasing the amount of light reaching the ground, which then promote the growth of young seedling (Kilawe et al. 2018, Epila et al 2017). Seasonality impacted germination and development of *M. eminii* seeds in our study. In the dry season, unlike in the wet, seed germination was inhibited more strongly by shade the invasive species distribution. Sufficient availability of moisture during the wet season also triggered higher germination of *M. eminii* seeds to the extent of overcoming the impact of shading as was shown in our study. With advent of the rainy season and of the new flush of leaves, light levels drop and seedlings may die in the shade unless they are subjected to a gap size of minimum 300m^2 (Kilawe et al. 2018). Epila et al. (2017) stated similarly that water availability is a limiting factor for the occurrence of *M. eminii* and they found that 97% of the mapped *M. eminii* occurred in sites receiving an annual mean rainfall of more than 1000 mm. As reported by Boy (2005), Ye and Wen (2017) in seedling establishment and overall environmental adaptation, seed germination represents an important development phase playing a critical role in invasion ecology.

5. Conclusion

We found that *Maesopsis eminii* seed germination, particularly during the dry season, was higher under lower shade levels. The ability to germinate not only under high light but also under a wide range of environmental conditions is one of the distinguishing features for most plant species and allows exploitation of broad niches, during which competition for resources is low. Our study suggests that light levels might act as a barrier to the invasive capacity of *M. eminii*, particularly at germination stage. Hence shade might be limiting its colonization success and wide distribution range in forest ecosystems. This knowledge has important implications for predicting susceptible ecological niches and, hence, can foster proactive management strategies in the Amani Forest Reserve. However, the factors triggering invasive species success might vary at different stages of the invasion process. Given rapid climatic changes, knowledge of the germination behavior of native and alien species under natural conditions is crucial for predicting future plant community dynamics. Hence, management of *M. eminii* invasion needs to take into account light and water availability regimes in the future. This can be achieved through early detection during the wet season when the species germinates at its highest rate and through minimizing forest gaps and other disturbances that might create favorable light conditions for *M. eminii*.

Funding

This work was funded by the World Bank Centre for Research, Agricultural Advancement, Teaching Excellence and Sustainability (CREATES) project at Nelson Mandela African Institution of Science and Technology, Tanzania.

Acknowledgement

We are appreciative to Mrs. Mwanaid S. Kijazi, the Conservator of Amani Nature Forest Reserve for providing accommodation and permits during field work. Heartful thanks are also due to Mr. Donald Lubasha, Incharge of Kwamkoro forest station and Mr. Mrisho Kimweli, Supervisor, Amani Central Nursery for their valuable logistical, field support and silvicultural advice during this work.

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Conflicts of Interest Statement

Manuscript title: **Effect of Seasonality and Light Levels on Seed Germination of the Invasive Tree *Maesopsis eminii* in Amani Nature Forest Reserve, Tanzania**

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