Forest Ecology and Management 362 (2016) 20–28

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Life history traits predict the response to increased light among 33 tropical rainforest tree species

Malin Gustafsson [a,*], Lena Gustafsson [b], David Alloysius [c], Jan Falck [a], Sauwai Yap [c], Anders Karlsson [a], Ulrik Ilstedt [a]

[a] Swedish University of Agricultural Sciences, Department of Forest Ecology and Management, 901 83 Umeå, Sweden
[b] Swedish University of Agricultural Sciences, Faculty of Natural Resources, Department of Ecology, 750 07 Uppsala, Sweden
[c] Conservation & Environmental Management Division, Yayasan Sabah Group, P.O. Box 11623, 88817 Kota Kinabalu, Sabah, Malaysia

ARTICLE INFO

Article history:
Received 25 June 2015
Received in revised form 26 August 2015
Accepted 9 November 2015
Available online 5 December 2015

Keywords:
Canopy openness
Dipterocarpaceae
Gap dynamics
Tree seedling
Tropical forest

ABSTRACT

Rainforest restoration is an important application in today's multipurpose management of secondary forest. However, our knowledge of tree species' traits and responses to treatment is insufficient for foresters to make good decisions for sustainable management. The aim of our study was to see whether it is possible to predict tree species' responses to increased light based on species' traits, and to relate these responses to a possible pioneer–climax continuum of life history traits, also among species with presumed climax properties. We examined 33 taxa (including 19 from the dipterocarp family) replicated 20 times and randomly planted in lines over a 3 ha area in the interior of Sabah, Borneo. Four years after establishment we performed a canopy reduction treatment to increase the light conditions up to levels present in tree gaps in the forest. We created a PLS (Partial Least Square Regressions) model with the two predicted variables HGR (height growth response) and Q3 HGR (the 75 percentile of a species' HGR, interpreted as the potential HGR). The model captured 47% of the variation for the predicted variables. We found significant tree species' responses in height growth to the increased light. High specific leaf area, strong early height growth, high foliar N content, high leaved stem length and large crown were linked to fast growth, while high wood density and high foliar K content were associated with slow growth. We also found a trade-off between growth response and survival among the species. We conclude that climax tree species have specific life history adaptations along a pioneer–climax continuum, which can be predicted from species' traits. The importance of easily observed or extracted traits such as initial growth rate, specific leaf area and wood density for predicting growth suggests the possibility of fast screening of species with unknown characteristics, which could be of great value in practical forest management.

1. Introduction

Large parts of the world's tropical rainforests are degraded from logging, fires, and conversion into other land uses. In many regions, there is growing interest in restoring the structure and diversity of these forests (Brancalion et al., 2013; Chazdon, 2008; Gibson et al., 2011; Hector et al., 2011b). However, restoration efforts are hampered because we have limited knowledge of the ecology of rainforest tree species. Such knowledge is necessary for appropriate and successful forest management interventions. Out of at least 3000 known Bornean tree species, the dipterocarps (Dipterocarpaceae) are dominant in terms of numbers as well as biomass in late successional lowland evergreen rainforest (Ashton and Kettle, 2012; MacKinnon et al., 1996), and they are main timber species in SE Asia. Tropical timber species – the species that are removed during logging and therefore most in need of support during restoration – are usually late successional, shade tolerant hardwoods, often referred to as climax species (Whitmore and Burnham, 1975) (Fig. 1). Management strategies to boost tree diversity and biomass commonly involve planting and tending young trees of species with climax properties (Asner et al., 2003; Hector et al., 2011a; Martínez-Garza and Howe, 2003).

Key environmental drivers for tree growth and survival in tropical rainforests are light and nutrient availability. For regenerating seedlings in tropical lowland rainforests, light is often the primary limiting factor (Born et al., 2014; Rozendaal et al., 2006; Poorter, 1999), since only small amounts reach the forest floor under a closed canopy, although stochastic events (e.g. a tree fall or logging) may create short periods of increased light. Openings in the canopy are extremely important in allowing seedlings to acquire enough light in the dark understory: these gaps account for about

* Corresponding author.
E-mail address: malin.gustafsson@slu.se (M. Gustafsson).

http://dx.doi.org/10.1016/j.foreco.2015.11.017
0378-1127/

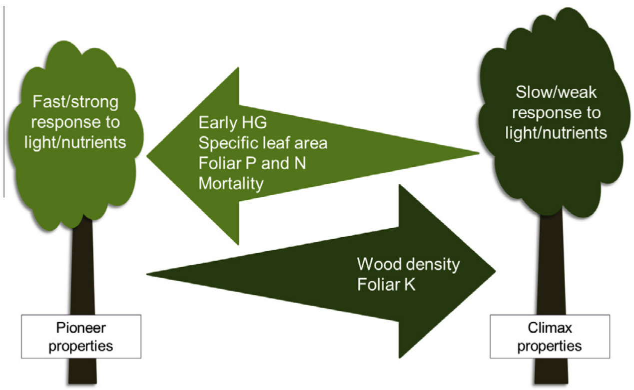

Fig. 1. Conceptual model of the pioneer–climax continuum. A continuum of tree species' resource investment strategies that are directed to either fast growth or better chance of survival; where species with clear climax properties (e.g. high wood density and foliar K content, and low specific leaf area and mortality) mainly invest in stability and resilience, while species with clear pioneer properties – at the other end of the continuum – invest in fast height growth (HG) and strong response to increased resources or environmental disturbance.

50% of the light that reaches the forest floor (Chazdon, 1988). The forest light conditions control photosynthetic activity, which is a major factor in the production of biomass (Niinemets and Valladares, 2004). Manipulation of the light environment, for example by girdling and removal of competing vegetation (Jennings et al., 1999), is common to enhance tree seedling growth and survival, and species-specific responses to changes in the light conditions have been recorded (Ådjers et al., 1998; Duclos et al., 2013; Romell et al., 2008). Even so, the number of studies of the light factor is limited and we are still far from being able to generalize about responses beyond a few tested species. Phosphorous (P) is the principle limiting nutrient in tropical forests on highly weathered soils, although potassium (K) and nitrogen (N) also influence tree growth and survival (Dieter et al., 2010; Palmiotto et al., 2004; Paoli et al., 2008).

Ecologists have long noted the existence of a growth–survival trade-off – often also referred to as the growth–mortality trade-off – among rainforest tree species (Ackerly, 2003; Poorter and Bongers, 2006; Sterck et al., 2006) with diverging life strategies – acquisitive or conservative. Long lived tree species with resilient climax properties such as high wood density (WD) and low specific leaf area (SLA) exhibit weak responses to available resources, slow growth and high foliar K content, i.e. their life history adaptation is to outlive rather than outgrow competition (King et al., 2006; Rozendaal et al., 2006). Fast growth, low WD and high P and N content in leaves, on the other hand, indicate early-successional pioneer properties with rapid response to available resources and high mortality (Poorter et al., 2008; Wright et al., 2010). There is no clear-cut distinction between pioneer and climax species (Clark and Clark, 1992; Wright et al., 2004), but instead a continuum representing a range of life histories (Born et al., 2014; Denslow, 1980; Whitmore and Burnham, 1975). A species' position along the pioneer–climax continuum may be predicted from its responses to change i.e. the life history traits. Knowledge concerning traits and responses to treatment can help in the selection of tree species for forest restoration. Tree traits, preferably ones that are easy to measure, can be used to assess species' performance and thus to identify species' responses to treatment (Hattori et al., 2013; Mouillot et al., 2013; Poorter and Bongers, 2006; Poorter et al., 2008).

Our study involved juveniles of 33 tree species, of which most are locally described as climax species and 19 are dipterocarps, in a field experiment with planted trees in Sabah, Malaysia. Earlier studies have focused on species' traits and growth performance among tree seedlings (Born et al., 2014) or saplings (Philipson et al., 2011) in controlled experiments, on seedlings in nursery experiments (Clark and Clark, 1992; Poorter, 1999) or on naturally regenerated trees (Rozendaal et al., 2006). The large number of species in our study – both dipterocarps and other important restoration species – provides an opportunity to analyze the variation in functional traits along the pioneer–climax continuum. We conducted a canopy reduction treatment 4 years after planting in order to study the growth response to increased light availability, and examine how the responses varied with tree species' traits. The canopy reduction treatment was conducted to imitate the gap dynamics of a tropical rainforest (Denslow, 1987), and this sort of treatment is applicable for practical enrichment planting projects.

We used traits to predict the tree species' responses in height growth to treatment (Table 1). Two measures of height growth response was used – height growth response (HGR) and the upper quartile HGR (Q3 HGR) – to predict the relationships under more and less limiting conditions regarding for example light and nutrient availability. Q3 HGR represents the response value at the 75th percentile of a species' HGR. We assumed that the individuals of a species that exhibited a more positive growth have been exposed to less limiting site conditions (an approach similar to Wright et al. (2010) who used the 95th percentile). In our analyses, Q3 HGR represents the inherent potential of a species to respond to the canopy treatment. We focused on height growth since it is an easily measured trait. Diameter growth at 1.3 m (DbhR) could also potentially be used, but at the time of measurement, only about 1/3 of the trees had reached 1.3 m in height.

The aim of the study described in this paper was to examine responses to increased light after a canopy reduction treatment in 33 presumed climax tree species in a lowland rainforest. We wished to test whether response variation could be explained by life history traits linked to the pioneer–climax continuum (Fig. 1), and whether the studied species could be positioned along this continuum. Our main hypothesis was that species with traits closer to those of pioneers (high SLA, M, N, P and low WD, K; see Fig. 1) would have a stronger positive response to the canopy reduction treatment than species with climax properties. In addition, we wanted to create a model for predicting tree species' response to treatment based on a number of easily acquired traits.

2. Method

2.1. Study area

In 1998, the 18,500 ha INIKEA Sow-a-seed Project restoration area was established with the main aim of restoring biodiversity through enrichment planting with a diverse selection of tree species. More than 80 native tree species have been used over the years, collected as seeds or wildlings in this lowland mixed dipterocarp rainforest of the Sg. Tiagau Forest Reserve in southeast Sabah (4°36′N, 117°12′E), Borneo. The climate is humid tropical equatorial with high precipitation throughout the year, even though a wetter season usually occurs from October to February (Peel et al., 2007). Measured mean annual precipitation in the project area was 2517 mm (SD 760 mm) for the years 2002–2013. The project area had been selectively logged when parts of it were severely affected by forest fires in the early 1980s. The remaining secondary forest held different levels of disturbance, from heavily disturbed areas with a large element of pioneer species and weeds, to more or less pristine forest patches. Most forests surrounding the INIKEA project had, at the time of the study, been logged and large areas had been converted into other land uses, mainly oil palm plantations.

We established a tree species field trial study (ca. 3 ha) in the interior of the INIKEA project in an area with an intermediate level