Population dynamics in a 6-year-old coppice culture of poplar II. Size variability and one-sided competition of shoots and stools

I. Laureysens, W. Deraedt [1], R. Ceulemans [*]

University of Antwerp, Campus Drie Eiken, Department of Biology, Universiteitsplein 1, B-2610 Wilrijk, Belgium

Abstract

Coppice cultures are characterised by a high stool and shoot density. Studies on density-dependent mortality, and intraspecific competition in crowded populations have mainly focused on non-woody species. We investigated intraspecific competition in a coppice culture of poplar (*Populus* spp.). A high-density plantation with 17 poplar clones was established in April 1996, coppiced (i.e. cut back) in December 1996 and subsequently grown for 4 years (1997–2000). High stool mortality was observed in the establishment year. Frequency distributions of stool and shoot size, and the relationship between shoot biomass and shoot density was determined for the different clones during the 4-year rotation. Stool mortality was not correlated with stool density. In the paper it will be argued that stool competition was probably very low, although increasing by the end of the rotation. Stool mortality was caused by *Melampsora* rust infections, implicating that process based yield models for poplar SRC should take into account rust infections. Skewness and inequality of shoot size distributions were very high at the start of the rotation, but progressively decreased during the course of the experiment. No self-thinning line was found, although high shoot mortality was evident for all clones. Therefore, it might be argued that shoot elimination within a stool was not due to light competition, but to another physiological mechanism within the stool/dominant shoot.

1. Introduction

Within the framework of the greenhouse effect and the depletion of fossil fuels, biomass energy has an important role to play (Hall et al., 1997). Woody energy crops, e.g. poplar and willow, additionally offer an alternative use for the land taken out of agricultural production and have a positive impact on biodiversity, and on soil quality and stability (Gordon, 1975; Perttu, 1995; Isebrands and Karnosky, 2001). These trees are usually planted as hardwood cuttings, and are grown in carefully tended high-density (10,000–20,000 trees ha^{-1}) plantations for rotations shorter than 15 years, and as such are referred to as short rotation crops

* Corresponding author. Tel.: +32 3 820 22 56;
fax: +32 3 820 22 71.

E-mail address: reinhart.ceulemans@ua.ac.be (R. Ceulemans).

[1] Present address: Johnson & Johnson, Pharmaceutical Research and Development, Turnhoutseweg 30, B-2340 Beerse, Belgium.

(Dickmann and Stuart, 1983). To promote sprouting of many shoots per tree, and hence increase final biomass production, the trees are usually coppiced at the end of the establishment year (Sennerby-Forsse et al., 1992; Macpherson, 1995). Coppicing refers to the cutting of a tree at the base of its trunk, mimicking natural disturbance processes like fire and resulting in the re-generation of new shoots from the stump and/or roots (Blake, 1983). The early growth rate of coppice shoots is very high, because they benefit from the existing root system. The high number of shoots per unit area results in a rapid leaf area development, leading to fast crown closure and efficient utilisation of space (Blake, 1983; Sennerby-Forsse et al., 1992).

Several empirical and mechanistic models have been developed to predict poplar growth and biomass production (Ceulemans and Isebrands, 1996). How-ever, none of these models are capable of predicting biomass production of short rotation coppice systems (SRC) over the long term, since there is very little information regarding the dynamics of competition and self-thinning in poplar coppice stands. Standing biomass in coppice stands depends upon the number of living stems/shoots and their individual size. In addition, for certain wood uses, e.g. pulp production, wood of certain dimensions is needed. It is therefore essential to be able to predict stool and shoot mortality, and as such the number of shoots and their size frequency distribution at any given time. In order to obtain these predictions, insights should be gained in the processes and mechanisms of intraspecific competition. Most research on intraspecific competi-tion thus far has focused on non-woody species; few studies have concentrated on monoclonal even-aged single tree stands, e.g. *Pinus* and *Picea* (e.g. Laessle, 1965; Ford, 1975; Cannell et al., 1984), *Eucalyptus* (Tomé et al., 1994; Soares and Tomé, 1996) and *Populus* (Roberts and Richardson, 1985). Studies on competition in SRC are rare: we found only one study on poplar SRC (Van Hecke et al., 1995) which reported on border effects and size inequality.

Cannell et al. (1984) defined competition in the following terms: ''Competition in plant monocultures implies that the supply of environmental resources (light, water and nutrients) falls below the combined demands of the plants, and that the environmental resources are shared unequally between plants in relation to their size''. At stand level, size asymmetry

and inequality can be used as an indication of one-sided competition. In the early stages of stand development in even-aged monocultures, plant size distributions are approximately normal because of the normal distribution of seed size (Ford, 1975; Mohler et al., 1978). Several years after a stand has been established, plant size distributions become positively skewed as a result of the exponential growth of the individuals, and size asymmetry will be amplified by one-sided competition (Weiner and Thomas, 1986). One-sided competition, i.e. a disproportionate share of resources (relative to size), results in the growth suppression of the smaller individuals and conse-quently in an increasing size inequality (Weiner, 1985; Weiner and Thomas, 1986). Two-sided competition, on the other hand, implies a perfect sharing of resources relative to size, resulting in an unaffected or lower size inequality (Weiner, 1985). One-sided competition is usually related to competition for light, and two-sided competition to the sharing of water and nutrients (Soares and Tomé, 1996). Size asymmetry and inequality will progressively increase – possibly resulting in a bimodal distribution (Ford, 1975; Mohler et al., 1978) – up to the time of self-thinning. Density-dependent mortality will be highest for the individuals in the lower size classes, resulting in a progressively lower size asymmetry and inequal-ity (Mohler et al., 1978; Hara, 1985; Weiner and Thomas, 1986; Knox and Peet, 1989).

Yoda et al. (1963) found an empirical relationship, i.e. the 'self-thinning rule', between mean plant biomass and plant density after a stand starts self-thinning. The rule defines an upper boundary of mean plant biomass for a given plant density in an even-aged pure plant stand. In a self-thinning population, the decrease in density when plant size increases follows a power equation:

$$w = kN^{-a} \tag{1}$$

where w is the mean plant biomass (g), N the plant density (m^{-2}) and a and k are the constants. Constant k is species and environment specific; $a = 3/2$ is the hypothesized self-thinning coefficient, resulting in a straight line with slope 1.5 when mean plant biomass is plotted against plant density on logarithmic scales. Several authors have re-evaluated the rule, and con-cluded that the slope is variable and varies with aspects of the biology of the plant, and that a straight