Abstract Only recently have studies addressed the effect of early-colonizing vegetation on tree seedling survival and growth during secondary succession in tropical old fields, and few studies have elucidated the physiological responses of tree seedlings to different vegetational communities. We compared growth and various photosynthetic parameters for seedlings of four rain-forest tree species, Cedrela tooduzii, Inga punctata, Ocotea whitei, and Tapirira mexicana, growing in areas of pasture grass and shrubs in early-successional abandoned pasture in Costa Rica; in addition, we made measurements for two species in forest gaps. We tested the general hypothesis that early-colonizing shrubs facilitate growth of forest tree seedlings. Specifically, we measured microclimate, growth, CO₂ assimilation, stomatal conductance, photosystem II quantum yield (ΦPSII), and xanthophyll pigment pools for all seedlings. Photosynthetic flux density (PFD) was higher under grass than shrubs or forest gaps, but was highly variable in each growth environment. For three of the four species, height growth was greatest in the grass compared to the shrubs and forest gaps; growth was similar below grass and shrubs for O. whitei. Photosynthetic capacity, apparent quantum yield, and stomatal conductance did not vary across habitats, but light compensation point and PFD at light saturation tended to be higher in the grass compared to forest and shrub growth environments. Water use efficiency differed across growth environments for three of the species. For plants in ambient PFD and dark-adapted plants, the efficiency of excitation energy transfer through PSII was lowest for plants in the grass compared to shrubs and forest gaps and also differed across species. Measurement of steady-state responses of ΦPSII to increasing PFD indicated a significant effect of growth environment at low PFD for all species and significant effects at high PFD only for I. punctata. All species exhibited a high degree of midday xanthophyll de-epoxidation in the different growth environments. Xanthophyll pigment pool size on an area basis was highest in the grass compared to shrubs and forest gaps for all four species. The results suggest that shrubs do not provide a facilitative effect for growth or photosynthesis for ~1.5-year-old seedlings of these four species. We conclude that site differences in success of tree seedlings during succession are a result of complex interactions of facilitation and competition and are not simply based on physiological responses to PFD.

Keywords Competition · Facilitation · Photoprotection · Photon flux density · Xanthophylls

Introduction

The effects of existing vegetation on the establishment of forest trees in abandoned old fields has been studied extensively in the temperate zone (e.g., McDonnell and Stiles 1983; Pickett et al. 1987; de Steven 1991a, 1991b; Myster 1993; Berkowitz et al. 1995). Only recently, however, have studies focused on the role of shrubs in tropical old-field succession (e.g., Vieira et al. 1994; Aide et al. 1995; Holl et al. 2000). Research in the temperate zone suggests that early successional shrubs may have variable effects on different stages of seedling regeneration (Pickett et al. 1987; Walker and Chapin 1987; Myster 1993; Callaway and Walker 1997). For example, shrubs often enhance seed dispersal by animals and woody seedling establishment (Werner and Harbeck 1982; McDonnell and Stiles 1983; Li and Wilson 1998), but shrubs may also compete with larger seedlings for nutrients, light, and water (Walker and Chapin 1986; Putz and Canham 1992; Berkowitz et al. 1995). Similarly, the few studies of succession in abandoned agricultural land in the tropics suggest that early successional shrubs enhance seed dispersal compared to areas of grass (Saab and Petit 1992; Vieira et al. 1994; Cardoso da
The primary objective of this study was to compare the effects of pasture grasses and early-successional shrubs on the growth, photosynthesis, water relations, PSII efficiency, and xanthophyll pigment content for four species of tropical tree seedlings. For comparative purposes we also measured these factors for two of the species in forest treefall gaps. If early-colonizing shrubs facilitate growth via impacts on photosynthesis and photoprotection for certain tree species, then shrubs may play an important role in determining patterns of tropical forest succession in abandoned pastures.