

Clonal growth in *Ailanthus altissima* on a natural site in West Virginia

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Abstract: The exotic tree *Ailanthus altissima* is usually confined to open sites. As an exception, *Ailanthus* established in a densely closed forest in West Virginia, which was analyzed with the aim to elucidate possible pathways of persistence in forest succession of this light-demanding pioneer species. Demographic analysis revealed a seedling mortality of 100%. Instead, the understory is populated by clonal ramets, ranging from one to more than 19 yr of age, with a mean of 5 yr. Growth averages only 0.11 m/yr, and height is correlated with age. This clonal growth contrasts with the performance of *Ailanthus* on open sites. The possible ecological benefits of establishing a ramet bank in a resource-poor habitat are considered in terms of space occupation of a pioneer species.

Keywords: Demography; Exotic tree; Growth strategy; Ramet bank; Shade tolerance.

Nomenclature: Clarkson (1966).

Introduction

Ailanthus altissima (Mill.) Swingle was introduced between 1740 and 1750 from China to Paris, and has ever since become a common 'weedy tree' naturalized all over the temperate and meridional zones of the world (Hu 1979). It is a characteristic woody pioneer of disturbed sites, particularly in cities (Santamour 1983; Kowarik & Böcker 1984; Pan & Bassuk 1986; Sachse et al. 1990). *Ailanthus* is an early successional species which is supposed to invade natural vegetation only if some form of disturbance has provided safe sites for its establishment. It may also invade naturally disturbed flood-plain vegetation, rocky outcrops, and similar open habitats (Kowarik 1983; Airola & Buchholz 1984; Gutte et al. 1987). The absence of *Ailanthus* from closed forests has been explained by its low shade-tolerance, as compared to late successional species (Grime & Jeffrey 1965; Feret 1985). In tree fall gaps, a population may establish if seeds are available (e.g. Kim 1990), but during succession it will be subjected to competition from taller trees casting shade. As a comparison, in the

Appalachians the similar American pioneer tree *Robinia pseudoacacia* is replaced during forest succession in only ca. 30 yr (Boring et al. 1981).

Although the same situation may be expected for *Ailanthus* in its original distribution area, its performance in natural forest succession is still unknown. Particularly information on natural Chinese vegetation is lacking, while natural forests invaded by *Ailanthus* as an alien species are rare. One example of the latter situation was analyzed in West Virginia, where *Ailanthus* shows a high level of plasticity in clonal growth. Knowledge of the correlation between clonal growth strategies and the habitats in which they prevail is still fragmentary (de Kroon & van Groenendael 1990). The present paper will discuss some results of a demographical approach to the performance of *Ailanthus*, notably functional aspects of clonal growth in a densely closed forest compared to open urban sites. Possible pathways of persistence of *Ailanthus* as a light-demanding tree in natural forests are suggested as a stimulus for further research.

Study site and Methods

In West Virginia, *Ailanthus* usually invades disturbed sites (Clarkson 1966), but it also occurs in a forest at the foot of Seneca Rocks, an outcrop of Tuscarora Sandstone within the Monongahela National Forest (see McKoy 1988; Stephenson & Adams 1991 for geology, climate, and forest types of the area). Due to the destruction of the original forests in the late 19th century, this stand is not virgin, but no traces of recent man-made or natural disturbance were observed.

The floristic composition of the stand was documented by a phytosociological relevé (cf. Mueller-Dombois & Ellenberg 1974). In order to analyse the regeneration mode of *Ailanthus*, the demography of clonal ramets and of seedlings was analysed in a transect of 16 1-m² plots, including two older stems of *Ailanthus* (0.24 and 0.29 m DBH) at one end. The clonal origin of the ramets was ascertained by excavating sprouts and revealing

them as root-born shoots. They were easy to distinguish from seedlings. Annual extension growth in *Ailanthus* starts from lateral buds. Therefore, the minimal age of ramets could be determined non-destructively by counting the dead ends of branches providing an insight into the temporal dynamics of the clonal population.

Results

In addition to *Ailanthus*, 10 tree species formed part of the canopy, including *Acer saccharum*, *Tilia heterophylla*, and different *Quercus* species (Table 1). Like the native pioneer *Robinia pseudoacacia*, *Ailanthus* reached a height of more than 20 m. Both these species shared the upper canopy, but were lacking from the subcanopy which was characterized by *Tsuga canadensis*. Unlike *Robinia*, however, *Ailanthus* occurred in both the first and second shrub layers, and surprisingly, it dominated the ground layer.

The demographic analysis showed two different ways of regeneration. *Ailanthus* had produced seedlings as well as ramets of clonal origin, but only the latter were successful. The population in the ground layer was almost completely (96 %) of clonal origin. The few seedlings dated from the year of the field analysis.

The height of clonal ramets varied from 0.1 to 2.0 m (average height 0.52 m, sd = 0.32). The ramet density calculated for all plots was 3/m², that of seedlings was much lower, 0.13/m². The minimal age of ramets varied

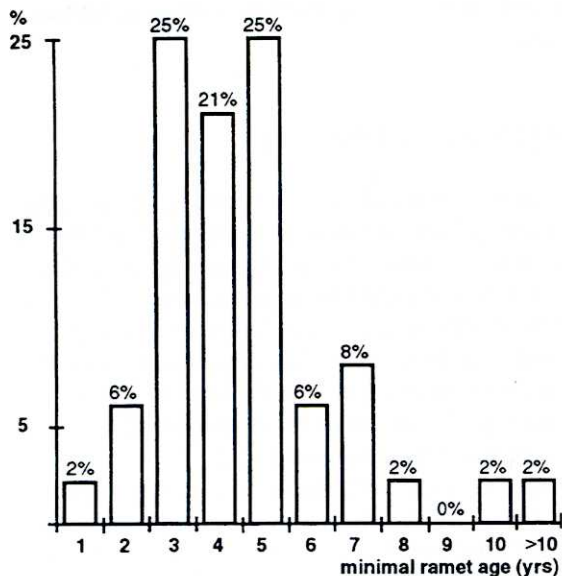


Fig. 1. Age structure of a ramet population of *Ailanthus altissima* at Seneca Rocks, West Virginia, determined by using the minimal ramet ages ($n = 48$ ramets from the ground and shrub layers, mean age = 4.7 yr, sd = 2.7)

from 1 - 19 yr (mean age = 4.7 yr, sd = 2.7; Fig. 1). Two dead ramets were counted within the transect. Ramet mortality was also observed outside the transect.

The height and the minimal age of ramets were correlated ($r = 0.85$). The tallest ramet (2.0 m) was also the oldest (at least 19 years). The average annual height increment was only 0.11 m (sd = 0.04). In addition to *Ailanthus*, seedlings of *Acer rubrum*, *Tilia heterophylla*, and *Quercus rubra* were found. 19 individuals had germinated in the year of field analysis, seven were older. In contrast, seedling mortality in *Ailanthus* had been 100%, because no seedlings from previous growing seasons were found.

Table 1. Vegetation relevé of a forest stand including *Ailanthus altissima* at Seneca Rocks, West Virginia (25 m × 25 m plot); cover of the tree-, shrub- and ground layers in %, species' cover recorded according to the scale of Barkman et al. (1964).

	Cover
Upper canopy (18 - 22 m)	80%
<i>Tilia heterophylla</i>	3
<i>Acer saccharum</i>	2b
<i>Quercus prinus</i>	2b
<i>Q. rubra</i>	2b
<i>Ailanthus altissima</i>	2a
<i>Robinia pseudoacacia</i>	2a
<i>Carya glabra</i>	2a
<i>Vitis</i> sp.	1a
Subcanopy (6 - 9 m)	40%
<i>Acer saccharum</i>	2b
<i>Tsuga canadensis</i>	2a
<i>Acer rubrum</i>	2a
<i>Ulmus americana</i>	1a
<i>Carya tomentosa</i>	1a
First shrub layer (2 - 5 m)	5%
<i>Ailanthus altissima</i>	1a
<i>Hamamelis virginiana</i>	1a
<i>Ulmus americana</i>	1b
Second shrub layer (0.9 - 2 m)	10%
<i>Ailanthus altissima</i>	2b
<i>Fraxinus pennsylvanica</i>	+r
<i>Corylus cornuta</i>	+r
Ground layer (< 0.9 m)	15%
<i>Ailanthus altissima</i>	2b
<i>Parthenocissus quinquefolia</i>	2a
<i>Acer rubrum</i>	2m
<i>A. saccharum</i>	+p
<i>Arisaema triphyllum</i>	+p
<i>Dryopteris marginalis</i>	+p
<i>Galium aparine</i>	+p
<i>Rhus toxicodendron</i>	+p
<i>Rubus</i> sp.	+p
<i>Smilax rotundifolia</i>	+p
<i>Tilia heterophylla</i>	+p
<i>Acer pennsylvanicum</i>	+r
<i>Alliaria officinalis</i>	+r
<i>Dioscorea villosa</i>	+r
<i>Impatiens</i> sp.	+r
<i>Polypodium virginianum</i>	+r
<i>Robinia pseudoacacia</i>	+r
<i>Rosa</i> sp.	+r
<i>Solidago</i> sp.	+r

