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REGENERATION BEHAVIOR OF COMPETING PLANTS AFTER CLEAR-CUTTING

A.U. Mallik, Y.L. Gong, and F.W. Bell

INTRODUCTION

Secondary succession, which follows forest harvesting, begins with the growth of herbs, shrubs, and trees and eventually leads to a mature forest. However, young, commercially important trees are often suppressed by undesirable plants, and the prolific growth of clonal shrubs and trees poses a particularly difficult obstacle for conifer regeneration. Many undesirable plants regenerate quickly via clonal expansion by rhizomatous growth, stem base sprouting, root suckering, and layering of branches. Often, these undesirable plants must be controlled to ensure conifer survival and growth in young plantations.

The efficiency of vegetation control methods can be enhanced by adjusting the conifer release treatments to the regeneration phase of the competing species when they are most vulnerable. This requires autecological knowledge of the competing plants, because the potential for rapid vegetative growth often depends on microclimatic conditions and a plant's ability to develop sprouts from dormant or adventitious buds. Numerous authors have emphasized the need for a better understanding of the autecology of noncrop species for effective control of competing vegetation and an enhancement of silvicultural success (Bell 1991, Wagner and Zasada 1991, Wagner 1993).

STUDY SITE AND METHODS

Research for this study was conducted in Block 164 of the Seine River Forest Management Area, 58 km north of Atikokan, Ontario. A 7-year-old jack pine (*Pinus banksiana* Lamb.) plantation that was experiencing competition from trembling aspen (*Populus tremuloides* Michx.), pin cherry (*Prunus virginiana* L. fil.), green alder (*Alnus viridis* spp. *crispa* [Ait.] Pursh), and beaked hazel (*Corylus cornuta* Marsh.) was selected. The regeneration behavior, population dynamics, and competitive ability of the competing species were studied. Stem density, age-related mortality, recruitment of stems, and the nature of above- and belowground clonal dynamics were determined through both nondestructive and destructive sampling.

Vegetative regeneration strategies were determined by excavating the rhizome and root systems of the four competing plant species. The crown diameter of the clone was determined before excavation. Eight individual plants each of trembling aspen, pin cherry, and green alder were excavated. Beaked hazel clones were difficult to excavate because of their complexity and intertwined rhizomes; therefore, only four of these were removed. For each of the excavated clones the following above- and belowground parameters were measured: crown diameter; age; number of new, old, and dead stems; depth of sprouting center; area of sprouting; intersprout distance; root/rhizome diameter at a 30-cm interval (50 cm in the case of aspen); rooting depth at a 30-cm interval; and the oven-dry weights of the shoot and of the root plus rhizome.

RESULTS AND DISCUSSION

Stem Density

During the period from 1992 to 1994, stem mortality was high in trembling aspen. Only 42 percent, 56 percent, and 59 percent of the total standing aspen stems were alive in 1992, 1993, and 1994, respectively (Table 1). Pin cherry stem density also declined over these 3 years. However, stem mortality was higher during 1993 and 1994 (41 percent and 53 percent respectively) than in 1992 (8 percent). In these two species, the number of dead stems outweighed the number of new stem recruitment. This reflects a strong

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self-thinning effect through natural mortality. Aspen stem density at this site was low (4 400 stems/ha) (Table 1) compared to others (e.g., 20 000 stems/ha and 12 400 to 14 800 stems/ha [Perala 1972]). Much higher stem density was observed in the case of green alder and beaked hazel (27 600 and 12 800 stems/ha, respectively) than for trembling aspen and pin cherry. Tappeiner (1971) reported 12 010 to 18 900 green alder stems/ha in red pine (*Pinus resinosa* Ait) and white pine (*Pinus strobus* L.) stands in northern Minnesota. Evidence of numerous dead shoots on trembling aspen roots was reported by Tappeiner (1982), who concluded that only a few of the original shoots survive to maturity. High stem mortality from high stem density was reported in trembling aspen by Bella (1986). Mortality rate and the ratio of live and dead stems of pin cherry, green alder, and beaked hazel were not reported in the literature.

Vegetative Regeneration Strategies

A comparison of clonal characteristics of above- and belowground components of trembling aspen, pin cherry, green alder, and beaked hazel indicates that trembling aspen and pin cherry have similar vegetative regeneration strategies, and that these are different from those of green alder and beaked hazel (Fig.1a–d). Crown diameter, number of shoots per clone/ramet, and the above- and belowground biomass of trembling aspen and pin cherry were significantly different from those of green alder and beaked hazel (Table 2). Aspen and cherry stems were also significantly taller than were those of green alder and beaked hazel. Pearson product-moment correlation coefficients of the growth parameters showed that the number of shoots and suckers of aspen per ramet was positively correlated ($r = 0.65$) with their shoot, rhizome plus root biomass, and crown diameter (Table 2).

The shoot height of pin cherry was negatively correlated with intersproutal distance, but positively correlated with shoot and root biomass and with crown diameter. For green alder, shoot height was correlated ($r > 0.55$) with the number of shoots per clone, with shoot and root plus rhizome biomass, and with crown diameter. There were also strong positive correlations among these vegetative parameters ($r > 0.85$) for beaked hazel. Ordination of the canonical variate analysis for the seven vegetative parameters placed the four species in two distinct groups (Fig. 2). The 95 percent confidence interval for each of the four means is represented by a circle with a radius $r = 2/\sqrt{n}$ (n = sample size). Overlapping of the circles indicates no significant difference between the species means. The trembling aspen and pin cherry group was significantly different from the green alder and beaked hazel group.

Table 1. Number of live and dead trembling aspen, pin cherry, green alder, and beaked hazel stems per hectare. Means were determined by sampling twelve 5-m x 10-m permanent subplots from 1992 to 1994.

	Number of stems (per ha)					
	1992		1993		1994	
Species	Live	Dead	Live	Dead	Live	Dead
Trembling aspen	4 580	3 200	3 550	3 800	2 500	3 800
Pin cherry	3 600	300	2 120	1 500	1 120	1 360
Green alder	27 580	1 560	25 600	4 920	25 920	3 600
Beaked hazel	14 600	320	11 400	1 600	1 436	2 000

Competition Strategies

With regard to competition strategies of the four species following initial establishment, trembling aspen and pin

Table 2. Clonal characteristics of the above- and belowground components of trembling aspen, pin cherry, green alder, and beaked hazel. Values are mean values of eight clones for each of the first three species and four clones of beaked hazel, ±S.E.

Species	Crown diameter (cm)	Root collar diameter (cm)	Intersprout distance (cm)	Shoot Number	Shoot Height	Dry biomass Rhizome and root (g)	Dry biomass Shoot (g)
Trembling aspen	77 a	2.7 a	61 a	2.8 a	184 a	410 a	461 a
	(8.4)	(0.4)	(16)	(0.4)	(17)	(89)	(93)
Pin cherry	77 a	1.4 a	53 a	2.3 a	146 a	242 a	238 a
	(12.4)	(0.3)	(20)	(0.4)	(14)	(46)	(42)
Green alder	140 b	13.7 b	—	14.0 b	105 b	947 b	624 b
	(13.7)	(1.5)		(1.4)	(14)	(142)	(82)
Beaked hazel	135 b	3.2 a	49 a	8.0 b	97 b	811 b	873 b
	(41.3)	(0.4)	(8)	(2.1)	(18)	(145)	(201)

Note: Values with different letters in the same column are significantly different ($P > 0.05$). Values in brackets represent standard error of the mean.

cherry reduce the light that reaches the crop plants by overtopping them. They also have a low root–shoot biomass ratio. This is known as the vertical competition strategy (VCS). In the case of green alder and beaked hazel, their dense clones consist of many short, aboveground shoots and dense, belowground roots and rhizomes. These compete horizontally with crop plants for space, nutrients, and moisture—a strategy termed the horizontal competition strategy (HCS). Where competing plants using both strategies are present in sufficient numbers on a site, the crop plants suffer from long-term competition. Vegetation control methods should be developed based on the proportion of VCS and HCS plants, and on their population dynamics, such as rate of clonal spread, height growth, stem mortality, and recruitment. Strategies concerning the vegetative spread of clonal plants have been described by several authors (Tappeiner 1971, Bunnell 1990, Huffman et al. 1994). However, none of these studies quantified the age-dependent mortality of vegetative shoots.

Clonal Dynamics of Green Alder

When the number of new, mature, and dead stems in alder clumps of various sizes were compared with stem age, it became apparent that this species expanded rapidly after forest harvesting. For approximately 5 years alder produced a high density of new and mature stems; then, this was followed by a decline in stem density (Fig. 3). Forest harvesting on the study site occurred 7 years prior to the commencement of this research. The high frequency of new and mature stems aged 5 to 12 years (i.e., 5 years pre- and 2 years postharvest) seems to indicate four things: namely, (i) the mature jack pine forest canopy may have been opening up, thereby creating microsites suitable for alder regeneration (Fig. 3a); (ii) with the removal of the forest canopy, alder clumps became vigorous due to rapid growth of preexisting stems and newly recruited sprouts (Fig. 3b); (iii) increased mortality of alder stems was initiated by self-thinning (Fig. 3c); and (iv) false growth rings can be counted. Furthermore, the presence of 23- to 30-year-old alder stems in some clumps indicate that, at the time of harvest, these stems were 16 to 23 years old. This means that alder clumps can perpetuate with reduced vigor in mature forests.

Following a demographic study of speckled alder (*Alnus incana* spp. *rugosa* [DuRoi] Clausen), Huenneke (1986) reported that long-term persistence of alder clumps is

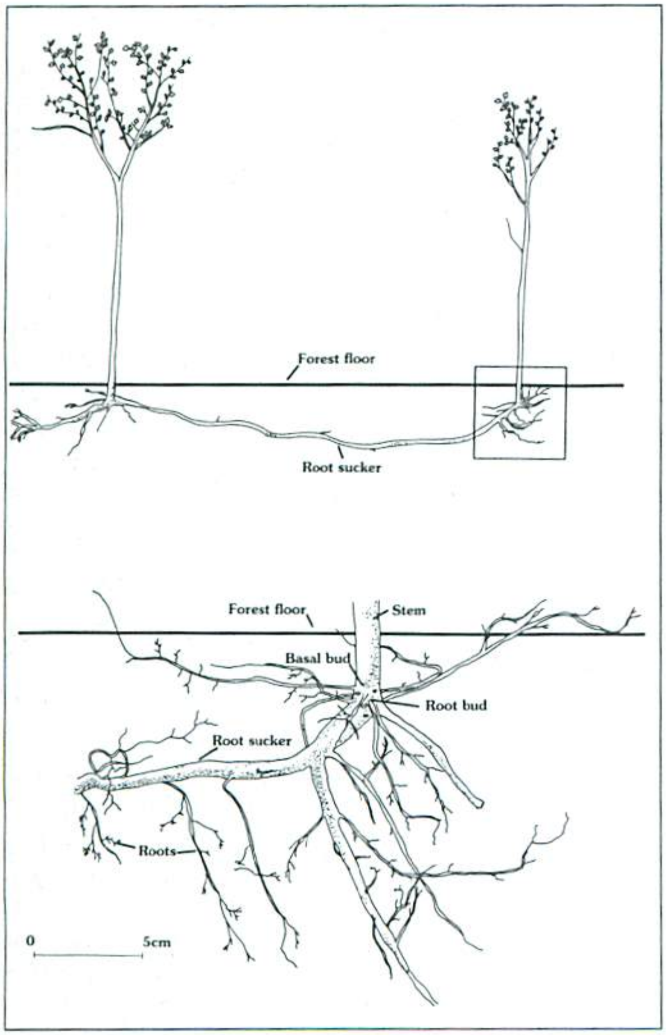

Figure 1a. Main organs of vegetative reproduction of trembling aspen.

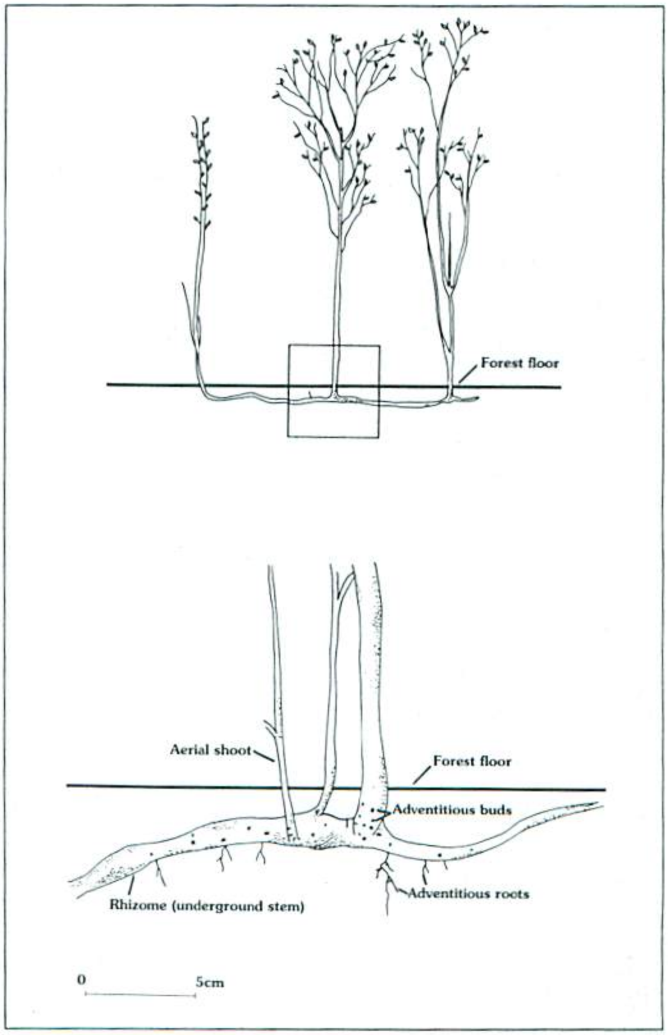

Figure 1b. Main organs of vegetative reproduction of pin cherry.

possible through vegetative regeneration by basal sprouting. During the study the author encountered no alder seedling recruitment, nor was the death of an entire alder clump observed. In the present study, most stem recruitment occurred between a 5-year pre- and 2-year postharvest period. The high belowground to aboveground biomass ratio of alder (Table 2) indicates its high potential for vegetative sprouting. The sprouts that were recruited immediately after harvesting remained most vigorous. There was a decline in alder stem density starting 2 years after harvesting (Fig. 3b). The decrease in the number of live stems and the concomitant increase in the number of dead stems was recorded between 1992 and 1993. In 1994, however, the number of live stems was very similar to that of 1993, with reduced stem mortality (Table 1). For alder to remain vigorous it must recruit new vegetative sprouts or establish new seedlings. However, a reduction in stem density in the clump does not necessarily mean reduced vigor or competitive ability of the plant, since the remaining live stems can offer substantial competition if they are growing vigorously. Seedling regeneration in alder was not very common—only five seedlings in twelve 5-m x 10-m plots were observed over a period of 3 years.

Excavation of alder clumps revealed a swollen, corm-like structure at the base of the stems from which new sprouts originate. Corms from large clumps showed decay in the older parts and progressive growth in the newer parts, often with one or more daughter corm(s) connected with short (5–10 cm), horizontal rhizomes buried under the litter. The daughter corms and the living tissue of the parent corm were capable of producing new sprouts. This type of vegetative regeneration mechanism, where sprouts originate from swollen stem bases, is common in ericaceous plants such as *Calluna vulgaris* (L). Hull, *Erica cinerea* L., and *Arctostaphylos uva-ursi* (L.) Spreng. when subjected to periodic disturbance (Mallik and Gimingham 1985). However, the progressive growth and decay of alder corms with age may keep the clumps alive for a long time. On the other hand, plants such as *Calluna vulgaris* undergo morphologically distinct growth phases (Barclay-Estrup 1970), and in their degenerative phase lose their sprouting ability and die. Thus, tree seedling establishment is possible during the degenerate phase of *C. vulgaris* growth (Khoon and Gimingham 1984).

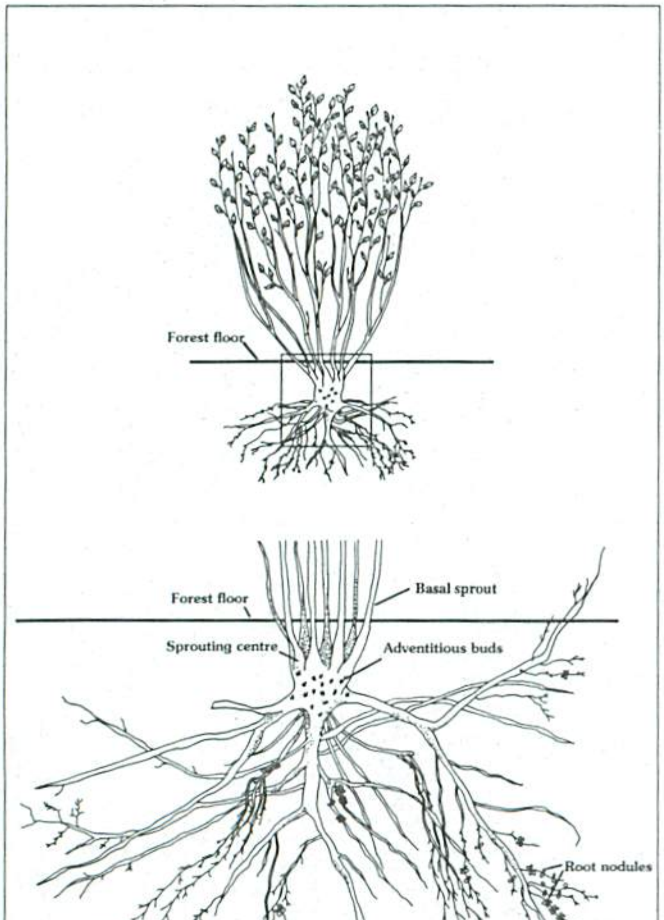

Figure 1c. Main organs of vegetative reproduction of green alder.

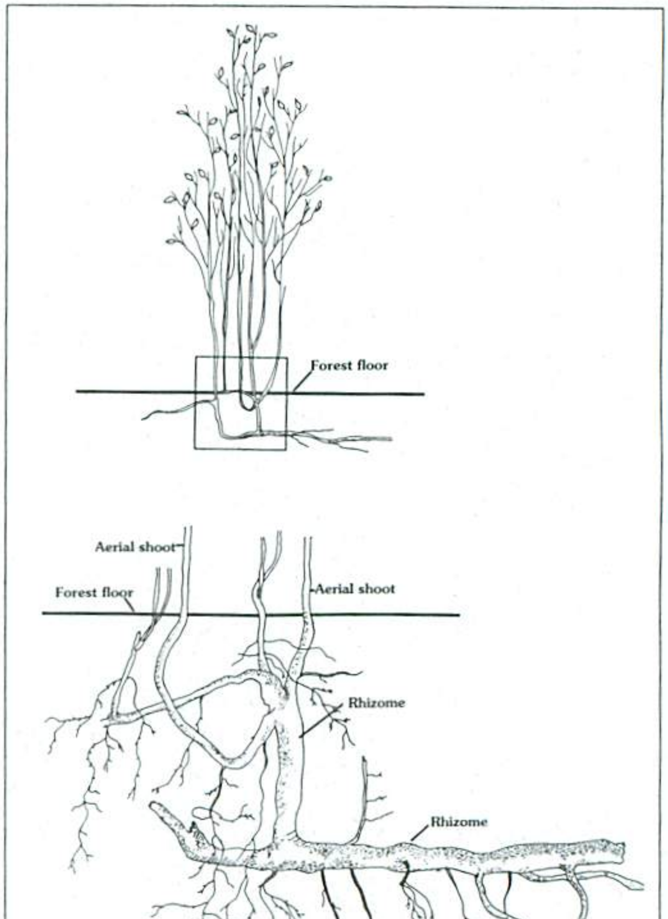

Figure 1d. Main organs of vegetative reproduction of beaked hazel.

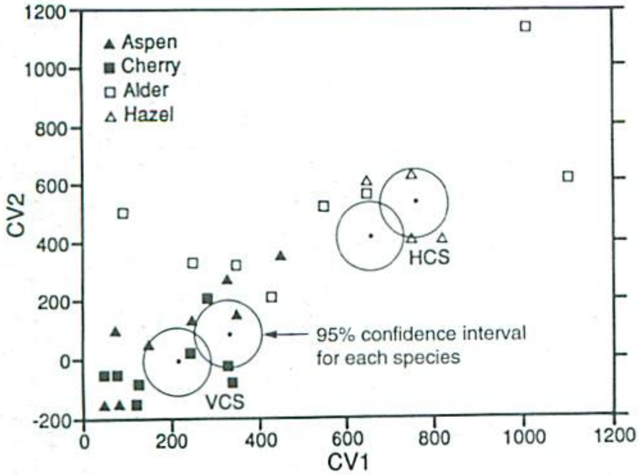

Figure 2. Canonical scores and means of vegetative parameters of four competing species. The 95 percent confidence interval for each species mean is represented by a circle. Overlapping of the circles indicates that there is no significant difference between them.

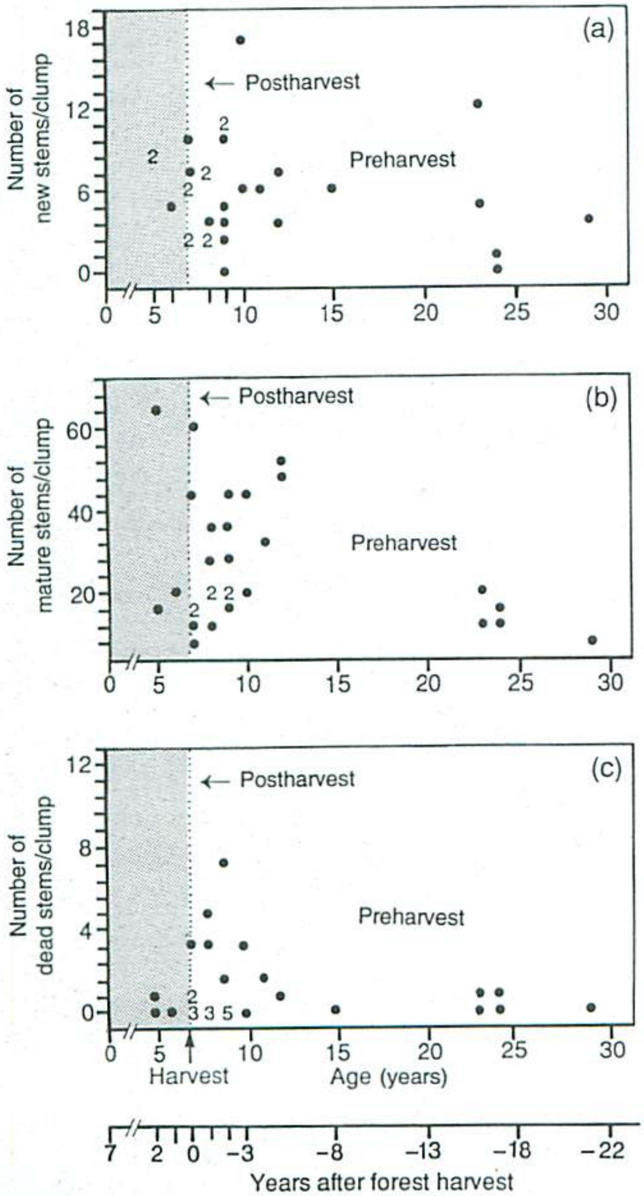

Figure 3. Age-dependent clonal dynamics in green alder. Note that the clones between the ages of 6 and 12 years have the maximum number of dead, mature, and new stems.

CONCLUSIONS

Understanding the regeneration strategies of competing plants can provide useful insights for predicting their competitive abilities. The density and proportion of plants belonging to the VCS and HCS groups identified in the present study can determine the nature and duration of competition on a site.

Evidence supporting the vertical and horizontal competition strategies (VCS–HCS concept) in this study is based upon the regeneration characteristics of only four competing plants. However, as more autecological information on other plants becomes available, the VCS–HCS concept should gain stronger support. Detailed information on species regeneration characteristics, root–shoot architecture, age-related spread, and mortality is essential for predicting competition.

Self-thinning of stems over time by natural mortality, and the degeneration of clones from old age are important phenomena to consider before applying any vegetation control intervention.

The need and timing of vegetation control on a site, based on the critical growth period of crop trees in relation to the degree and duration of competition, should be documented. If the nature of the competition is acute, and the vigor of competing plants is not likely to decline for some time, then vegetation control may be necessary. On the other hand, if the competition level is low and the population dynamics of the clonal plants are such that after a certain period of time their competitive abilities would decline without significant damage to the crop trees, then the site may not require vegetation control.

The regeneration characteristics of competing plant species and the level of tolerance of crop plants to competition will determine the need, timing, and method of vegetation control. The age-related clonal dynamics of species such as green alder can tell forest managers how long the competing species will remain vigorous in a mature stand.

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