Bigleaf maple seedling establishment and early growth in Douglas-fir forests[1]

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Survival, age and height distributions, and stocking of bigleaf maple (*Acer macrophyllum* Pursh) seedlings were studied in 1- to 250-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands in western Oregon to identify the stages in stand development in which bigleaf maple is most likely to establish successfully from seed. Maple seedling emergence averaged 30–40% where seeds were planted and protected from rodents but was typically <2% for unprotected seeds. Seedling survival after 2 years was highly dependent on canopy density, measured by percent sky. Average 1st-year survival of seedlings originating from planted, protected seeds was highest in clearcuts (1–2 years old, 36% survival, 56% sky) and pole-size stands (41–80 years old, 30% survival, 17% sky) with sparse understories and canopies. It was lowest in young stands with dense canopies (20–40 years old, 4% survival, 8% sky) and old stands (81–250 years old, 14% survival, 13% sky) with dense understories. Naturally regenerated populations of bigleaf maple seedlings, which occurred in aggregations (0.005–0.04 ha in area), were most abundant (up to 10 000/ha) in pole-size Douglas-fir stands. Although seedling size distributions within stands had a strongly inverse J shaped form, size distributions within aggregations appeared more normal (bell-shaped). Seedling age rarely exceeded 15 years. Seedlings grew slowly in the understory, often reaching only 25 cm in height after 8–10 years, and were intensively browsed by deer. Naturally regenerated seedlings were virtually absent from clearcuts, probably because of dense competing vegetation and lack of seed caused by poor dispersal and seed predation. The "window" for the most successful establishment of bigleaf maple seedlings appears to begin after canopy thinning and end before forbs and shrubs invade.

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La survie, la répartition des classes d'âge et de hauteur, ainsi que le coefficient de distribution des semis de l'Érable à grandes feuilles (*Acer macrophyllum* Pursh) ont été étudiés dans des peuplements de Sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) âgés de 1 à 250 ans dans l'ouest de l'Oregon afin d'identifier les stades de développement des peuplements dans lesquels cet érable est le plus susceptible de s'établir avec succès à partir de la graine. L'émergence des semis d'érable a été en moyenne de 30 à 40% lorsque les graines étaient semées et protégées des rongeurs, mais elle était typiquement inférieure à 2% pour les graines non protégées. La survie des semis après 2 ans dépendait essentiellement de la densité du couvert foliacé, mesuré en pourcentage de découvert. La survie moyenne des plantules âgées de 1 an issues de graines semées et protégées a été la plus forte dans les coupes à blanc récentes (datant de 1 à 2 ans, 36% de survie, 56% de découvert) et dans les perchis (âgés de 41 à 80 ans, 30% de survie, 17% de découvert) pourvus de couverts et de sous-bois épars. Elle fut la plus faible dans les jeunes peuplements (âgés de 20 à 40 ans, 4% de survie, 8% de découvert) pourvus de couverts denses et dans les vieux peuplements (âgés de 81 à 250 ans, 14% de survie, 13% de découvert) pourvus de sous-bois denses. Les populations naturellement régénérées de semis d'Érable à grandes feuilles, qui se rencontraient en agrégats (surfaces de 0,005 à 0,04 ha), étaient les plus abondantes (jusqu'à 10 000/ha) dans les perchis de Sapin de Douglas. Bien que la répartition suivant la grosseur des semis dans les peuplements avait une allure en forme de J fortement inversé, la répartition suivant la grosseur dans les agrégats semblait normale (en forme de cloche). L'âge des semis dépassait rarement 15 ans. Les semis croissaient lentement en sous-bois, atteignant souvent seulement 25 cm de hauteur après 8–10 ans, et ils étaient fortement broutés par les cerfs. Les semis naturellement régénérés étaient virtuellement absents des coupes à blanc, probablement à cause de la végétation compétitive dense et du manque de semences provoqué par la mauvaise dispersion et la prédation des graines. La « fenêtre » qui permet le meilleur établissement des semis d'Érable à grandes feuilles semble débuter une fois que le couvert foliacé s'est éclairci et se terminer avant l'envahissement par les broussailles et les morts-bois.

[Traduit par la revue]

Introduction

Bigleaf maple (*Acer macrophyllum* Pursh) is an abundant hardwood in the Douglas-fir region of the Pacific Northwest. In Oregon, it is common in the Coast Range and in the western Cascade Mountains in a wide range of environments (Zobel *et al.* 1976). On upland sites, bigleaf maple is typically mixed with conifers, often constituting up to 20% of stand basal area; it rarely occurs in pure stands.

Bigleaf maple is well known for its vegetative reproduction. Basal sprouts (up to 50–60/stump), which originate from cut or burned maple trees, may grow 1–2 m/year for their first 3 years. Sprouts rapidly occupy available growing space and easily overtop planted conifer seedlings (Roy 1955). Consequently, bigleaf maple sprouts are often hand slashed or sprayed with herbicide in commercial conifer plantations in Oregon.

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TABLE 1. Description of the Douglas-fir stands in which survival, growth, and distributions of bigleaf maple seedlings were studied

No. (and location[a]) of stands	Stand age-class (yr)	Basal area (m^2/ha) Douglas-fir	Bigleaf maple	Other trees[b]	Herb and shrub cover (%)
	Study of survival of naturally regenerated seedlings (1983 cohort)				
7 (M)	Pole-size (41–80)	21–42	2–6	0–3	—
7 (M)	Old (81–250)	20–40	2–20	0–6	—
	Study of germination of sown seed and seedling survival (1984 cohort)				
3 (M)	Clearcut (1–2)	0	0	0	21–57
2 (M)	Young (20–40)	30–63	2–12	—	—
4 (M)	Pole-size (41–80)	18–59	4–10	—	—
3 (M)	Old (81–250)	60–70	3–14	0–7	—
	Study of seedling age, height, and stocking				
5 (MPA)	Young (20–40)	19–35	1–8	0–3	3–48
12 (MPA)	Pole-size (41–80)	13–36	1–6	0–17	18–84
7 (MPA)	Old (81–250)	19–40	1–10	0–4	35–77

[a]M, McDonald Forest or Dunn Forest; P, private land; A, H.J. Andrews Experimental Forest.
[b]Includes grand fir (*Abies grandis* (Dougl.) ex Lindl.), Oregon white oak (*Quercus garryana* Dougl. ex Hook.), and red alder (*Alnus rubra* Bong.).

Little is known about regeneration of bigleaf maple from seeds. The seeds are large (2 cm long), heavy (7165 seeds/kg) double samaras (Olson and Gabriel 1974) which germinate during winter. Both recent germinants and older seedlings are frequently seen in the understory of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests.

Bigleaf maple seedlings growing in McDonald Forest in the central Oregon Coast Range were significantly more abundant, taller, and older in small forest openings than on adjacent sites under dense forest canopy (Sabhasri and Ferrell 1960). There is no other published information on the establishment of bigleaf maple from seed; however, seedlings of two maple species of eastern North America, which are also found in forest understories, have been studied in more detail. Striped maple (*Acer pensylvanicum* L.) seedlings growing in hardwood forests survived well in the understory up to about 15 years of age, after which they died unless disturbance to the overstory provided additional light (Hibbs 1979). An inverse J shaped, or negative exponential, distribution for seedling populations (Hett and Loucks 1971) or a power function for entire populations from seedlings to mature trees (Hett 1971) best describes the stocking–age relationship of populations of sugar maple (*Acer saccharum* Marsh.) in the understory of maple forests, suggesting continuous germination and recruitment of new seedlings and mortality of older ones.

We hypothesized that bigleaf maple seedlings are readily established in the understory of 30- to 60-year-old Douglas-fir stands, occurring in unevenly distributed aggregations. We further hypothesized that establishment is limited by low light levels in Douglas-fir stands <30 years old and by competition from a dense layer of shrubs, forbs, and grasses in stands >60 years old. We tested these hypotheses in mixed hardwood–conifer stands ranging in age from 1 to over 250 years, by conducting experiments on bigleaf maple seed germination and seedling survival, recording factors causing mortality, measuring canopy density and soil moisture, and surveying seedling age and height distributions and stocking. Information on establishment of bigleaf maple from seed, thus far absent from the published literature, could be useful to forest managers for preventing competition between bigleaf maples and conifers and for developing maple or mixed maple – Douglas-fir management regimes.

Methods

Study-site descriptions

The study was conducted principally on Oregon State University's McDonald and Dunn forests, west-central Oregon (44°40′N, 123°20′W), in stands typical of commercial forests in the eastern part of the Oregon Coast Range. Annual average rainfall is 1300 mm, air temperature is 9–12°C, and the frost-free season is 165–200 days (Knezevich 1975). Elevation ranges from 175 to 400 m. The soils, derived principally from basalt, are 75–150 cm deep. Twenty-four stands were used for evaluating age, height, and stocking of bigleaf maple seedlings. Seventeen were on McDonald and Dunn forests, four were located on private lands a few kilometres west, and three were on the H.J. Andrews Experimental Forest in the Oregon Cascade Mountains, where precipitation is higher and forests are somewhat more productive than on the principal study sites (Table 1). The stands represented the wide range of overstory and understory densities and species composition common in this part of the Douglas-fir region (Franklin and Dyrness 1973). Maple seed trees were present in all stands except clearcuts.

Seed germination and seedling survival

We studied survival and causes of mortality of a 1983 cohort of naturally regenerated seedlings that grew from a large 1982 seed crop and of a 1984 cohort originating from sown seeds.

Cohort from 1983

In spring 1983, shortly after numerous natural seedlings emerged, a permanent remeasurement plot (0.005–0.03 ha) was established for each stand in seven pole-size (41–80 years) and seven old (81–250 years) stands (Table 1). On each plot, 30–50 emergent seedlings were marked for identification, and their survival was monitored monthly over three growing seasons and two winters. At the end of 2 years, the height of 5–10 seedlings per plot was measured, and rooting depth of 20 two-year-old seedlings growing adjacent to several remeasurement plots was assessed by digging seedlings out and carefully separating their roots from the soil.

Cohort from 1984

Germination of sown seeds and survival of resulting seedlings were studied in 12 stands selected to represent a broad range of ages and densities (Table 1). Overstory Douglas-fir and bigleaf maple stocking in the pole-size and old stands was similar to that for the 1983 cohort. Three plots per stand were established in

TABLE 2. Average percent emergence of bigleaf maple seedlings grown from protected and unprotected seeds planted in Douglas-fir stands of different age-classes (1984 cohort)

	Clearcut (1–2 yr)	Young (20–40 yr)	Pole-size (41–80 yr)	Old (81–250 yr)
Protected seed	29.3*d*	41.3*e*	35.9*de*	41.6*e*
	(3.7)	(1.9)	(1.4)	(3.0)
Unprotected seed	1.6*ab*	0.4*a*	4.9*bc*	0.4*a*
	(0.6)	(0.3)	(1.4)	(0.2)

NOTE: Means followed by the same letter within both rows and columns do not differ significantly ($p \leq 0.05$, Tukey's test). Standard errors are in parentheses.

September 1983, each plot containing (*i*) 75 bigleaf maple seeds planted in a rodent exclosure (a circular cage 15 cm tall × 75 cm in diameter, 0.2 × 0.2 cm wire mesh, covered on top, and set 5–10 cm into the ground) designed to prevent seed predation, and (*ii*) a row of 75 uncaged seeds planted about 5 cm apart, adjacent to the exclosure. All seeds were collected in late September, the time of natural seedfall, from 10 trees on the McDonald and Dunn forests. Seeds with externally obvious defects were discarded. Seeds were sown on the day of collection to ensure their viability (Olson and Gabriel 1974), by inserting the dewinged samaras 1 cm into the duff or soil. According to viability tests (tetrazolium method of Grabe 1970) on a subsample of 200 seeds, 60% were sound at the time of planting. In total, 5400 seeds were sown.

Seedling emergence and mortality were monitored beginning in March 1984, both inside and outside the exclosures, and continuing at 2-week intervals until June. Exclosure lids were removed in June after emergence. Emergence, i.e., the number of recently germinated seedlings visible above the forest floor, was used as an index of germination, because identifying germinants below the forest floor would have required excessive disturbance. Beginning in June, survival of bigleaf maple seedlings was monitored monthly over two growing seasons and one winter. Mortality was attributed to predation (seedlings that had browsed roots and tops or were entirely missing), desiccation (withered and wilted seedlings), fungal attack (damping off or evidence of decay on roots and stems), or unknown over-winter causes. In addition, the height of 5–10 seedlings per plot was measured at the end of 1 year.

Canopy density

Canopy density was estimated in August by photographing the canopy above each remeasurement plot (1983 cohort) and rodent exclosure (1984 cohort) with a 35-mm camera (7.5-mm focal length, fisheye lens) mounted horizontally 1 m above the center of the plot or exclosure and analyzing the negative, Kodalith-derived slides, using a technique described by Chan *et al.* (1986). This technique yields estimates of percent sky, i.e., the area not obscured by foliage, which is correlated with photosynthetically active radiation. Thus, percent sky serves as an index of canopy density. In all forested stands, canopy photographs were taken directly above the remeasurement plots or rodent exclosures; in clearcuts, the camera was placed on and parallel to the ground, so that the photographs would account for any shading by low vegetation.

Soil moisture

Soil samples were collected monthly from June to September in 1983 and 1984 at three points on each remeasurement plot (1983 cohort) or at one point outside each of the three rodent exclosures per stand (1984 cohort). Samples were drawn from the entire profile between 1 and 30 cm, the zone occupied by 1st-year bigleaf maple seedling roots. Percent moisture was determined gravimetrically on 75- to 100-g samples of the fraction <2 mm, dried at 105°C for 48 h. Subsamples of each September sample were placed on a ceramic plate extractor to determine moisture content at soil moisture tensions of −0.5 and −1.5 MPa (Richards 1949). Soil moisture tension for each stand was then calculated from soil moisture content, with an equation derived separately for each stand, from a logistic regression of the three pairs of moisture content values measured at the two soil moisture tensions.

Seedling age and height distributions and stocking

Natural populations of bigleaf maple seedlings were studied in 24 Douglas-fir stands (Table 1). All stands had a relatively uniform Douglas-fir canopy (19–40 m^2/ha basal area) over an area of at least 4 ha, and had one or more bigleaf maple seed trees per hectare.

Standwide survey

Fifteen or more transects (1 × 30 m) were randomly located in each of the 24 stands. At two points on each transect, basal area by species was measured with a 20-factor prism and understory cover was ocularly estimated. Along the length of each transect, we recorded the number of bigleaf maple seedlings in each of six height classes (up to 5 m, which was our demarcation between maple seedlings and maple trees) and noted browsing damage as severe (multiple stem forking), moderate (single stem forking), or none. Average seedling age for each height class was estimated by counting bud scars or annual xylem rings on a subsample of 5–10 seedlings per height class in each stand. From a sample of 50 seedlings we found that 85% of the ages estimated by counting scars or rings agreed within 2 years. In addition, we thoroughly searched for bigleaf maple seedlings in eight clearcuts near the 24 Douglas-fir stands.

Aggregation census

In 8 stands (41–250 years old) of the 24 surveyed standwide, we censused 2 or 3 aggregations (each 0.005–0.04 ha in area) per stand of densely stocked bigleaf maple seedlings and measured the height, age, and degree of browsing of all seedlings in each of the 22 aggregations.

Data analysis

For the 1983 cohort, percent survival for each observation date was calculated as the number of live seedlings divided by the number of seedlings initially tallied. Differences in average percent survival after 1, 2, and 3 years among stands of the two Douglas-fir age-classes were compared using *t*-tests ($p \leq 0.05$). For the 1984 cohort, percent germination was calculated as the total number of emergent seedlings divided by 75 (the number of seeds sown) and percent survival for each observation date as the number of live seedlings divided by the number of emergent seedlings. Differences in percent germination and survival after 1 and 2 years were determined with a split-plot design and Tukey's test ($p \leq 0.05$).

Data from all plots for each cohort were analyzed with stepwise linear regression to determine the effect of percent sky, a transformation of percent sky, soil moisture content, and soil moisture tension at the end of summer on 1st- and 2nd-year survival for the 1983 cohort and 1st-year survival for the 1984 cohort.

From the standwide survey data, average numbers of maple seedlings in each of the six height classes were compared among stands of the three Douglas-fir age-classes, using one-way analysis of variance and Tukey's test ($p \leq 0.05$). Mean numbers of seedlings per height and age-class in the 22 aggregations were summarized graphically for each stand.

Results

Seedling emergence

Protection with rodent exclosures significantly ($p \leq 0.01$) affected maple seedling emergence. Where seeds were protected, average emergence of seedlings was significantly ($p \leq 0.05$) greater in the old (41.6%) and young (41.3%) stands than in the clearcuts (29.3%), but did not differ among old, young, and pole-size (35.9%) stands (Table 2). Where seeds were unprotected, average emergence of seedlings was significantly ($p \leq 0.05$) greater in pole-size (4.9%)

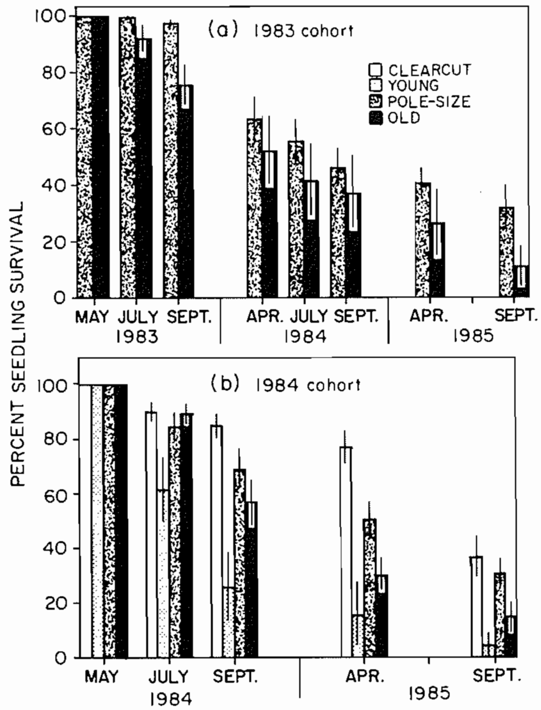

FIG. 1. Survival of (*a*) 1983 and (*b*) 1984 cohorts of bigleaf maple seedlings in clear-cut (1–2 years), young (20–40 years), pole-size (41–80 years), and old (81–250 years) Douglas-fir stands in western Oregon. Vertical bars represent standard error.

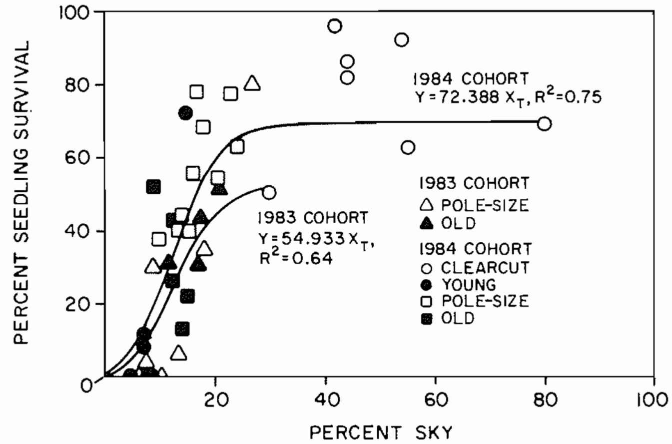

FIG. 2. Survival of bigleaf maple seedlings growing under Douglas-fir stands of different age-classes after 1 year (1984 cohort) and 2 years (1983 cohort) in relation to percent sky estimated from canopy photos. Percent sky data were transformed using the equation $X_T = 1/\{1 + \exp[3 - 24(\%\ \text{sky}/100)]\}$.

than in young (0.4%) or old (0.4%) stands but not in clear-cuts (1.6%). No seedlings emerged the 2nd year in any exclosure; all seeds not taken by predators apparently either germinated the 1st year or decayed. The highest emergence rate for protected seeds in any exclosure was 51%, somewhat less than the 60% viability determined by the tetrazolium test.

Seedling survival and growth

Survival of maple seedlings from the 1983 cohort in pole-size and old Douglas-fir stands did not differ significantly after 2 years (Fig. 1*a*). Survival ranged from 0% on a plot with 10% sky and a forest floor thick with maple litter and substantially undermined by rodents, to 80% on a very open plot (27% sky).

Average 1st-year survival rates of maple seedlings in the 1984 cohort, measured in mid-April (~1 year after germination), were significantly greater in clearcuts (77%) than in young (15%), old (29%), or pole-size (50%) stands (Fig. 1*b*). Survival in pole-size stands was also significantly greater than in young stands; other comparisons by age-class were not significant. After a second growing season, survival in all age-classes was considerably reduced, but with one exception, the statistical rankings remained the same. The large drop in survival on clearcuts can be attributed to an influx of herbaceous vegetation during the 2nd year, which dramatically diminished the light intensity reaching maple seedlings on some plots.

A primary cause of seedling mortality in both cohorts (48–59%) was predation, either by rodents, which clipped roots underground or in many cases pulled whole seedlings down into burrows, or by slugs (*Ariolimax* spp.) and other invertebrates, which browsed above ground. Of all seedling deaths, 19–40% occurred over winter for no obvious reason. Deaths due to desiccation for the 1983 cohort averaged only 10%, probably because soil moisture remained high during summer; for the 1984 cohort, they averaged 20%, possibly because summer moisture levels dropped. Deaths due to fungi or disease (2%) occurred only in young stands.

Average seedling height after 1 year ranged from 6.0 cm in clearcuts to 7.7 cm in old stands, and differences among stands were not significant. Height growth of unbrowsed seedlings during the second growing season was slow; average total seedling height (± SE) was only 6.8 (0.5) cm in pole-size stands and 6.1 (0.7) cm in old stands. The plot containing the tallest seedlings, 12.6 (1.2) cm, also had the highest seedling survival after 2 years and the highest percent sky. Average taproot length after 2 years was 19.8 cm (range 11–39 cm).

Relationship of maple seedling survival to Douglas-fir canopy density

Although 1st-year (April 1985) survival (Y) for the 1984 cohort was linearly correlated ($R^2 = 0.44$) with percent sky (X), a graph relating survival to percent sky seemed more steplike than linear. As percent sky increased, survival improved only marginally at first, then rose rapidly to near maximum level. Therefore, percent sky data were transformed with the equation $X_T = 1/\{1 + \exp[3 - 24(\%\ \text{sky}/100)]\}$, where X_T = transformed percent sky, which improved the correlation ($R^2 = 0.75$, $p \leq 0.01$) (Fig. 2). This transformation assumes an inflection point at 12.5% sky, an indication that there may be a threshold below which most 1-year-old maple seedlings will die. Thus, for a stand in which $X = 5$ and $X_T = 0.1418$, this regression predicts a 1st-year survival rate of 10%; where $X = 12.5$ and $X_T = 0.5000$, it predicts 36% survival; and where $X = 25$ and $X_T = 0.9526$, it predicts 69% survival. Because the shape and position of the fitted curve are largely determined from plots in the 0–30% sky range and because seedling survival on plots with >40% sky appears to vary independently of percent sky, this model is not recommended for predicting seedling survival percentages for stands with >40% sky.

A step function was not found in the 1983 cohort data because few plots had been established under either very dense or very open canopies. Survival was poorly related

TABLE 3. Average number of bigleaf maple seedlings in each height class, and average seedling age, by Douglas-fir age-class, in the standwide survey

Douglas-fir age-class (yr)	Height class (cm)					
	0–25	26–50	51–75	76–100	101–200	201–500
	No. of maple seedlings per hectare					
Young (20–40)	522*ef*	23*abc*	0*a*	0*a*	0*a*	9*ab*
Pole-size (41–80)	6303*g*	293*e*	82*d*	48*cd*	22*bc*	6*ab*
Old (81–250)	1493*f*	41*bcd*	25*bc*	15*bc*	15*bc*	10*ab*
	Age of maple seedlings (yr)[a]					
Young (20–40)	1.6*a*	11.0*c*	—*	—*	—*	na
Pole-size (41–80)	4.7*b*	11.1*c*	11.2†	12.7†	12.1†	27.0†
Old (81–250)	2.4*a*	11.0*c*	13.5†	14.5†	na	na

NOTE: For each seedling characteristic, means followed by the same letter within both columns and rows do not differ significantly ($p \leq 0.05$, Tukey's test). *, No seedlings in this category were available for measurement; †, too few seedlings for statistical comparison; na, age not available because of extensive browse damage.

[a] Maple seedling age ranges: 1–18 years under young Douglas-fir stands; 1–29 years under pole-size Douglas-fir stands; 1–20 years under old Douglas-fir stands.

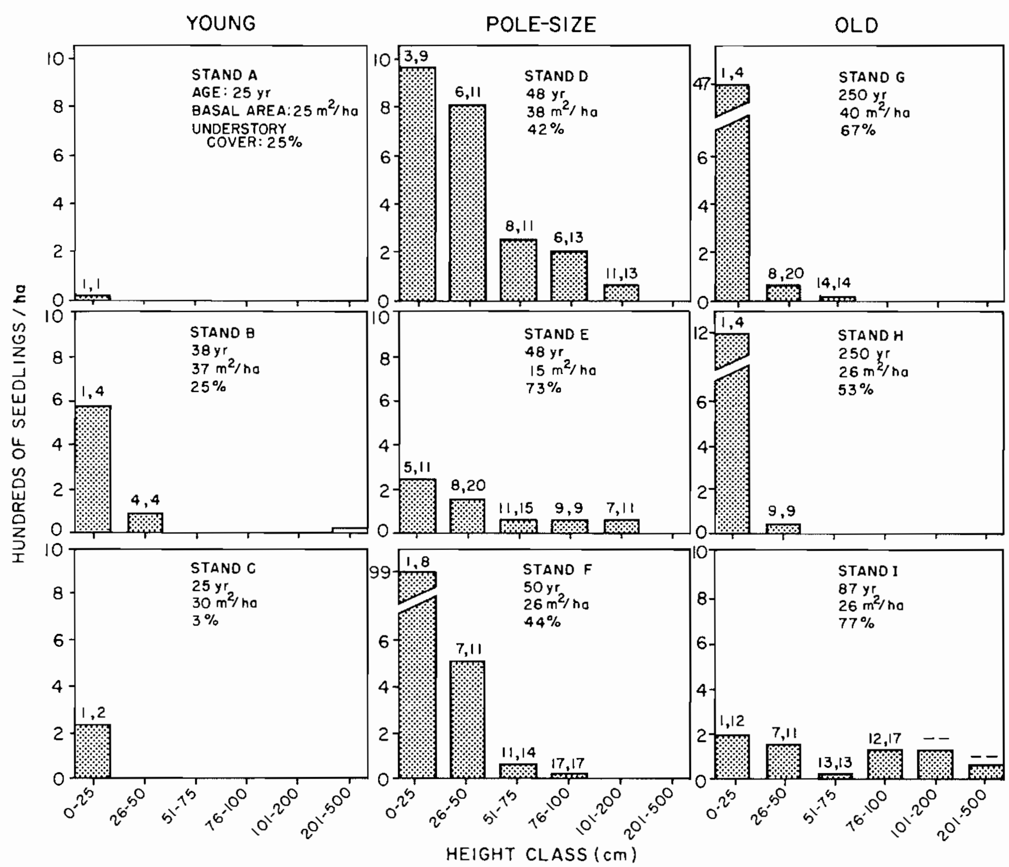

FIG. 3. Frequency, by height class, of bigleaf maple seedlings growing in 9 of the 24 Douglas-fir stands (3 per age-class) sampled in the standwide survey.Numbers above the bars are minimum and maximum seedling ages for each height class in the stand.

to percent sky after one growing season, but the relationship improved after two seasons (R_2 = 0.64, Fig. 2). The closeness of the values from the two curves over the domain 0–25% sky suggests that where light intensities are low, most maple seedlings die during the 1st year.

The timing of mortality also seems related to canopy density. In each Douglas-fir age-class, survival dropped off abruptly during the 1st year; seedlings in dense young stands died first, followed by those in less dense old and pole-size stands (Figs. 1, 2).

Relationship of maple seedling survival to soil moisture

Soil moisture levels during the 1983 and 1984 growing season were strikingly different. During summer 1983, rain fell intermittently until mid-July; then, except for 3 days in late August, no rain fell until early October. During summer 1984, no rain fell from late May until mid-September. In 1984, soil moisture averaged 29% by August 1, but in 1983 it did not reach this level until mid-September. Soil moisture tension did not fall below −1.5 MPa in either year.

Soil moisture tension in September 1984 varied significantly

($p \leq 0.05$) among stands. It was lower in old (−0.32 MPa) than in pole-size (−1.15 MPa) stands but did not differ among clearcut (−0.95 MPa) and young (−0.85 MPa) stands. Neither soil moisture content nor soil moisture tension in September was correlated with survival of either cohort, and in a stepwise regression, neither contributed any additional predictive power to the models based solely on percent sky.

Seedling age and height distributions and stocking

Standwide survey

The largest number of maple seedlings was found in pole-size Douglas-fir stands and stocking was quite variable, ranging from 600 to 43 000 seedlings/ha. In the first four height classes (seedlings up to 1 m tall), seedling density was significantly ($p \leq 0.05$) greater in the pole-size stands than in either the young or old stands (Table 3, Fig. 3). In all stands there were significantly more seedlings in the 0- to 25-cm height class than in any other class; in the pole-size stands, there were significantly fewer seedlings in each successively taller class (Table 3). Seedlings in the 0- to 25-cm class were significantly older ($p \leq 0.05$) in the pole-size stands (average 4.7 years) than in the young (1.6 years) or old (2.4 years) stands, and the range of seedling ages (1–29 years) was broadest in the pole-size stands.

Young Douglas-fir stands contained very few maple seedlings >25 cm tall, and most seedlings were <4 years old. Seedling densities in the 0- to 25-cm class varied widely within and also among stands (22–1350/ha) (Fig. 3). Old stands had significantly more seedlings between 50 and 200 cm tall than did young stands; however, average age of seedlings 1–50 cm tall did not differ (Table 3). Height and age varied considerably in these old stands, as they did in the young stands. For example, stand I had 600 seedlings/ha from 25–200 cm tall, whereas stand H had just 50 seedlings/ha (Fig. 3).

We found bigleaf maple seedlings in only two of the eight clearcuts searched. In one, there were just two aggregations of naturally regenerated maple seedlings, and they were older than the clearcut. In the other, there were fewer than 20 one-year-old seedlings on 16 ha, and these probably originated from seedfall before clear-cutting. In any case, we never saw a wave of maple seedling regeneration in these clearcuts of the magnitude of that observed beneath Douglas-fir stands.

We found no evidence of animals caching seeds. Groups of two or more seedlings, all having germinated at the same spot, were never observed.

Aggregation census

Both the numbers of seedlings within aggregations and the sizes of aggregations were quite variable within and among stands. For example, in stand M, aggregations of seedlings ranged from 0.005 to 0.04 ha, and numbers from 30 to 1700/0.01 ha (Fig. 4). The age and height distributions of aggregations were also quite variable, even among aggregations within the same stand. Unlike the age and height distributions in the standwide survey, which tended to be somewhat inverse J shaped, especially in the pole-size stands (Fig. 3), those in the aggregation census had no consistent form (Fig. 4). For example, the age and height distributions in stand H range from approximately normal (aggregation C) to rather biomodal (aggregation A). These differences in stocking and structure among aggregations

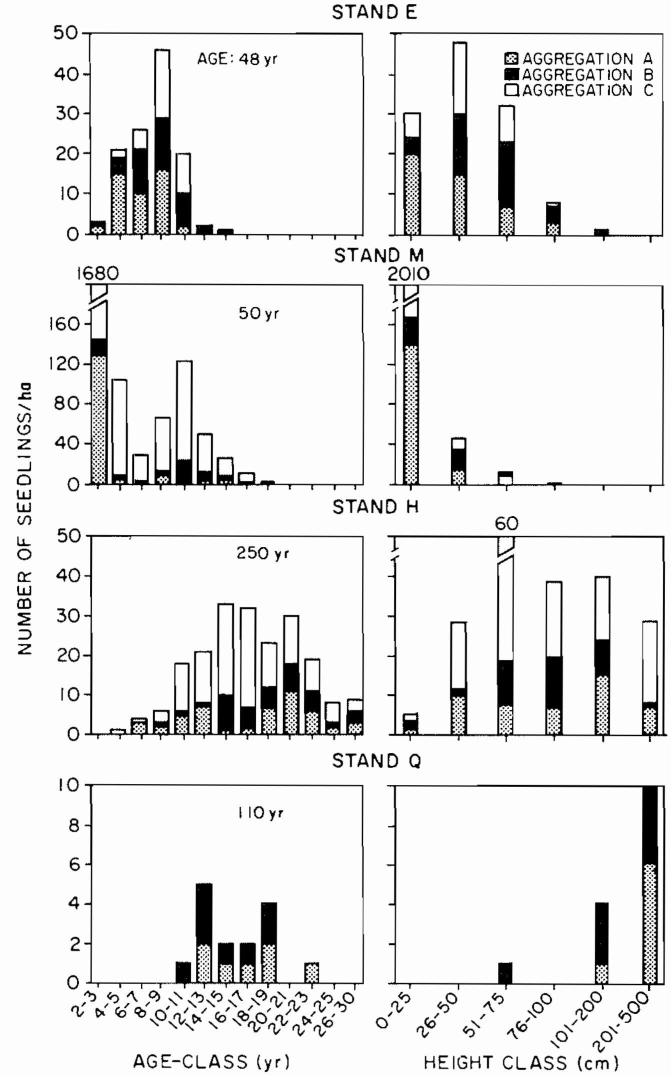

FIG. 4. Bigleaf maple seedling density, by 2-year age-class and height class, in two or three aggregations in four of the eight stands in which aggregations were censused.

indicate that conditions for seedling establishment and growth vary considerably within stands.

The ranges of maple seedling ages and the general shapes of the age distributions appear to be related to stand development and composition. Stand M is a pole-size stand which is undergoing self-thinning and whose understory is sparse; over 90% of the seedlings are <4 years old. In stand E, most maple seedlings are 6–10 years old, and a dense undergrowth of forbs and shrubs seems to be limiting establishment of new seedlings. We found seedlings older than 16 years only in stands H and Q, where windthrow had opened the canopy.

Numbers of bigleaf maple seedlings per age-class varied considerably. Seedlings from 1980 and 1982 seed crops were extremely numerous throughout the forest; no seedlings from the 1981 seed crop and only a few from the 1979 crop were found. We observed heavy seed crops on McDonald Forest in 1982 and 1985, but light ones in 1983 and 1984.

Effects of browsing on height growth

Browsing, probably by deer, substantially affected seedling growth. Over 60% (range 18–100%) of seedlings

>25 cm had been browsed, most of them several times. Because of repeated browsing, seedlings were often suppressed at about 1 m in height and as they grew older, developed numerous forks unless they succeeded in surpassing the reach of browsing deer. Of the 15- to 20-year-old seedlings, 90% had been browsed and were < 1 m tall. Even without browsing, seedlings grow slowly in the understory of closed-canopied stands; unbrowsed seedlings 25 cm tall were usually at least 8 years old. Because of browse damage, and probably variation in canopy density, we could not establish a general height–age relationship either for all stands or for individual stands, even if the most severely browsed seedlings were excluded. Browsing is generally limited to new growth. Both browsed and unbrowsed seedlings retain their original stem and do not become seedling sprouts by producing new stems as do tanoak (*Lithocarpus densiflorus* (Hook & Arn.) Rehd.) (Tappeiner and McDonald 1984) and other hardwoods.

Discussion

Predation on seeds appears to limit seedling establishment; where seeds were unprotected, only 0–16% of seedlings emerged, compared with 16–51% on protected plots. No seedlings emerged on the unprotected plots in clearcuts, indicating that predation may partly explain the virtual absence of seedlings from the eight clearcuts searched. Similar results have been reported for tanoak seedlings, which are not commonly found in clearcuts but which readily become established on them if tanoak seeds are protected (Tappeiner *et al.* 1986). After germination, rodent predation and moisture stress seem to be the principal causes of mortality, although average rates of maple seedling survival after 1 year were relatively high (15–77%) under all but the densest Douglas-fir stands.

Low light or other factors related to dense stands apparently limit seedling establishment. Percent survival increased from 0 to over 60 as percent sky increased from 5 to about 20, although further increases in light did not improve survival (Fig. 2). It is likely that the combination of low light and browsing (80% of the 10- to 29-year-old seedlings in the standwide survey were browsed) accounted for the mortality and slow, variable growth (< 1 m tall at 15–20 years) of bigleaf maple seedlings.

Bigleaf maple seedlings do not seem to be particularly shade tolerant. Their development in the understory resembles that of striped maple. Wilson and Fischer (1977) found that solar radiation regulated primordium development in striped maple seedlings and saplings. Light intensities of 6% of solar radiation in the open induced formation of bud scales, 18% promoted development of additional leaves, and 30–60% produced maximum height growth and leaf pair formation. Hibbs (1979) found that striped maple died at about 15 years of age unless the overstory was disturbed. The oldest bigleaf maple seedlings (10–29 years) we found were in a stand that had sustained windthrow 20 years earlier. In the standwide survey, we found few seedlings older than 15 years of age and none where the understory was dense (Table 3). Furthermore, survival of seedlings in both cohorts was especially poor in old stands with dense understories. Evidently, bigleaf maple, like striped maple, rarely survives for long beneath undisturbed overstory canopies and understory vegetation.

Successful bigleaf maple establishment is related to the stage of stand development. The poor survival, low stocking levels, and young age (< 4 years) of maple seedlings in 20- to 40-year-old Douglas-fir stands (for example, A–C in Fig. 3) suggest that light is not sufficient for seedling survival and that these stands are in the stem-exclusion stage of stand development (Oliver 1981). Indeed, we found that the number, age, and size of seedlings all increased in pole-size (41–80 years) stands, which are beginning the understory reinitiation stage. Thus, the "window" for the most successful establishment of bigleaf maple seedlings seems to be after natural, and probably silvicultural, thinning of Douglas-fir but before the development of the dense understory of forbs and shrubs characteristic of the late understory reinitiation and old-growth stages. However, more work is needed to determine how seedling establishment is affected by understory species composition and density.

Unlike sugar maple seedlings, which often have a relatively uniform distribution throughout the stand (Hett and Loucks 1971), bigleaf maple seedlings tend to aggregate in discrete groups in the understory of Douglas-fir stands. Fundamental differences in height distributions in stands sampled by both standwide survey and aggregation census highlight the patchy nature of successful maple regeneration. In stand H and to a lesser extent in stand E, the distributions are inverse J shaped; very few tall seedlings were observed along standwide transects (Fig. 3), yet proportionately more tall seedlings, as well as an order of magnitude more seedlings overall, were noted within aggregations censused in these same stands (Fig. 4). The unique age and size distributions and stocking levels of each aggregation (Fig. 4) suggest that conditions favoring establishment frequently change. Variation in canopy density, rodent and bird activity, seed supply, and density of understory shrubs and herbs may account for the varying age and height distributions of maple seedlings within stands.

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