Bitter cherry (*Prunus emarginata*) distribution, successional dynamics, and implications for the role of the seed bank

Brian B. Oakley and Jerry F. Franklin

Abstract: Bitter cherry (*Prunus emarginata* (Dougl.) Walp.) is a largely unstudied early successional tree native to the Pacific Northwest. We used multiple regression and regression tree analyses to identify the most significant variables describing the distribution of bitter cherry populations in the western Cascade Range of Oregon. To determine if bitter cherry relies on a soil seed bank for regeneration after disturbance, we compared successional patterns to direct measures of buried seed. Measurements from 78 sites ranging in age from 1 to 50 years since disturbance and 29 years of permanent plot data showed density, constancy, and cover were low in the first decade after disturbance and did not peak until the third decade. Based on these patterns, we inferred that bitter cherry is not an obligate seed bank species. We did find viable seeds stored in the soil (25.0 ± 6.4 seeds/m^2 (mean ± SE) on sites with >600 live stems/ha) but concluded that historical disturbance intervals greater than the length of time seeds can remain viable in the soil have limited bitter cherry regeneration from a seed bank and, as a result, its distribution and abundance. Bitter cherry may play an increasingly important role in Pacific Northwest forests given the large areas of early successional habitat created by frequent timber harvests.

Key words: H.J. Andrews Experimental Forest, seed bank, early succession, CART.

Résumé : Le cerisier amer (*Prunus emarginata* (Dougl.) Walp.) est un arbre natif de la région nord-ouest de la côte du Pacific, peu étudié et impliqué en début de succession. Les auteurs ont utilisé les analyses par régressions multiples et par dendrogrammes de régression pour identifier les variables les plus significatives, afin de décrire la distribution des populations du cerisier amer dans le Cascade Range occidental de l'Oregon. Pour déterminer si le cerisier amer a recours aux banques de semences du sol pour sa regénération après perturbation, les auteurs ont comparé les patrons de succession avec des mesures directes effectuées sur des graines enfouies. Les mesures obtenues sur 78 sites allant de 1 à 50 ans depuis la perturbation et 29 ans de recolonisation primaire montrent que la densité et la couverture demeurent faibles au cours de la première décade. Sur la base de ces patrons, les auteurs avançent que le cerisier amer n'est pas une espèce à banque de graine obligatoire. Ils ont trouvé des graines viables emmagasinées dans le sol (25,0 ± 6,4 graines/m^2 (moyenne ± é.t.) sur des sites portant >600 tiges vivantes par ha), mais ils concluent que les intervalles de perturbations plus grands que la longeur de temps que les graines peuvent demeurer viables dans le sol ont limité la regénération du cerisier amer à partir de la banque de graines, et conséquemment, sa distribution et son abonbance. Le cerisier amer pourrait jouer un rôle d'importance croissante dans les forêts de la région nord-ouest de la côte du Pacific, compte tenu des grandes surfaces d'habitat de succession primaire créées par les coupes forestières fréquentes.

Mots clés : forêt expérimental H.J. Andrews, banque de semences, début de succession, CART.

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Introduction

Early successional species utilize a variety of life-history strategies to respond to disturbance that may result in characteristic patterns of distribution and abundance. For example, soil seed banks have long been recognized as an important mechanism allowing rapid response to disturbance (e.g., Oosting and Humphreys 1940; Olmstead and Curtis 1947; Livingston and Allessio 1968; Moore and Wein 1977; Mladenoff 1990). Early successional species that may be represented in the predisturbance flora only by buried viable seeds can quickly become abundant following disturbance as the seed bank germinates in response to changes in light, temperature, or moisture (Olmstead and Curtis 1947; Marks 1974; Moore and Wein 1977).

In the Pacific Northwest, there are numerous examples of early successional species that rely on soil seed banks for establishment. Several species of *Ceanothus*, *Ribes*, and *Rubus* commonly proliferate during the early stages of succession by germinating from a seed bank (Cronemiller 1959; Gratkowski 1974; Orme and Leege 1974; Kramer and Johnson 1987; Morgan and Neuenschwander 1988). Bitter cherry

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B.B. Oakley[1] and J.F. Franklin. College of Forest Resources, University of Washington, P.O. Box 352100, Seattle, WA 98195-2100, U.S.A.

[1] Author to whom all correspondence should be addressed. e-mail: boakley@u.washington.edu

(*Prunus emarginata* (Dougl.) Walp.) has also been classified as an obligate seed bank species (Morgan and Neuenschwander 1988), but the role of the seed bank in the life history of bitter cherry has not previously been considered.

In this paper, the first detailed ecological study of bitter cherry, we examine the implications of the seed bank strategy for the distribution and successional dynamics of this Pacific Northwest native tree. We conducted our research in three stages. First, we quantified physiographic and biotic factors associated with the distribution of bitter cherry populations in the H.J. Andrews Experimental Forest (HJA) in the western Cascade Range of Oregon. Second, to characterize the successional dynamics of bitter cherry, we synthesized data from 78 sites in the HJA, 29 years of permanent plot measurements from a clearcut and burned watershed in the HJA, and historical records from throughout Washington and Oregon. Third, we compared these results to direct measures of seed bank density and spatial distribution to examine the role of the seed bank in bitter cherry distribution and successional dynamics.

Methods

Study area

The HJA is located on the western slope of the Cascade mountains in central Oregon, about 80 km east of Eugene. The HJA occupies a 6400-ha drainage with an elevational range from 410 to 1630 m. Topography is characteristic of the western Cascade Range with steep slopes and sharp ridges (Swanson and James 1975). Average annual precipitation is 2286 mm; winters are mild and wet, and summers are warm and dry (Bierlmaier and McKee 1989).

The lower elevations of the HJA (below 1000 m) typify the western hemlock zone with major components of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western red cedar (*Thuja plicata* Donn. ex D. Don) (Dyrness et al. 1976; Franklin and Dyrness 1973). Other tree species with more restricted distributions include sugar pine (*Pinus lambertiana* Dougl.), Pacific yew (*Taxus brevifolia* Nutt.), bigleaf maple (*Acer macrophyllum* Pursh), red alder (*Alnus rubra* Bong.), Pacific dogwood (*Cornus nuttallii* Audubon), and golden chinquapin (*Castanopsis chrysophylla* (Dougl) A. DC.). Above 1000 m, forests characteristic of the Pacific silver fir zone are dominated by Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), noble fir (*Abies procera* Rehd.), western white pine (*Pinus monticola* Dougl.), Douglas-fir, western hemlock, and western red cedar. Prior to the beginning of timber harvesting in the 1950s, about 65% of the HJA landscape was old growth with the remainder composed mainly of 50- to 150-year-old forests originating after fire (Teensma 1987; Spies et al. 1994). Since 1950, timber harvesting has created young managed stands on about 30% of the landscape (Spies et al. 1994).

Watershed 1 is a 100-ha watershed in the southwestern corner of the HJA; elevations range from 442 to 1082 m. Old-growth forests were clearcut between 1962 and 1966 and logging slash was broadcast burned during fall 1966. Prior to logging, 131 permanent 2 × 2 m plots were established at slope-corrected intervals of 30.5 m along six randomly located transects perpendicular to the main drainage of the watershed. Detailed descriptions of the Watershed 1 environment and permanent plot design can be found in Rothacher et al. (1967) and Dyrness (1973).

Distribution

Field methods

To quantify the distribution of bitter cherry in the HJA, all clearcut units were sampled except those with a history of herbicide use or precommercial thinning ($N = 78$). In each clearcut, perpendicular, bisecting transects 100 × 10 m and 110 × 10 m were established to provide a 2000-m^2 sampling area. A starting point for each transect was located on a map prior to visiting each site. If a random bearing led the transects across a road or out of a clearcut, the initial bearing was adjusted in 30° increments until a suitable starting point was found. Each transect started 5 m from the edge of any roadcuts to avoid sampling chronically disturbed vegetation. Within each transect, all live bitter cherry stems were tallied in 5-cm diameter classes, and eight variables were measured to be used as predictors in statistical models. Slope, aspect, elevation, and topographic position (lower slope, midslope, upper slope, or ridgetop) were recorded. Vegetative ground cover and canopy cover of woody shrubs and trees >2 m tall were visually estimated in 50-m subsamples based on the line-intercept method (Mueller-Dombois and Ellenberg 1974). Forest type (classified prior to disturbance) and stand age (time since disturbance) were summarized from an existing HJA database (Dyrness et al. 1971). Aspect was transformed with the function: $A' = \cos(45 - A) + 1$, where A is the aspect measured in degrees clockwise from north (Beers et al. 1966). All variables except aspect and elevation were treated as categorical variables.

Statistical methods

An ordinary least squares regression model was used to identify the predictor variables (modeled as dummy variables) that were most important in characterizing bitter cherry site preferences. The dependent variable, bitter cherry stem density, was log transformed to remedy unequal error variance and non-normality of the error terms (Neter et al. 1990). The normality of the transformed data was confirmed using D'Agostino's test at $\alpha = 0.05$ (Zar 1984).

Forward stepwise regression (Neter et al. 1990) was used to add each variable to a null model. Variables and interaction terms were added or dropped from the model if doing so resulted in a significant ($\alpha = 0.10$) improvement. The residuals were plotted against each of the independent variables and the predicted values to test for heterogeneity and non-normality of the regression error terms (Zar 1984; Neter et al. 1990). Because the regression model was used to describe the distribution of bitter cherry in the HJA and was not intended for other contexts, a predictive equation was not developed.

A regression tree was also fit to the distributional data. Classification and regression trees (CART) are relatively new statistical procedures that offer a nonparametric alternative to regression (Breiman et al. 1984; Chambers and Hastie 1992; Venables and Ripley 1994). Although the log-transformed data were normally distributed and met the assumptions of a regression model, regression trees are generally more robust than multiple linear regression when dealing with categorical data (Venables and Ripley 1994). With CART, data are classified by successively subdividing into increasingly homogenous groups. At each partitioning step, the new groups of data are examined separately along the multivariate axes of the predictor variables and further partitioned (Chambers and Hastie 1992). This process, called binary recursive partitioning, results in a model illustrating the relative importance of the predictor variables in terms of the dependent variable.

To ensure that the regression tree was both robust and easily interpretable, cross validation and pruning were used. Cross validation averages the results of $N - 1$ regression trees generated with a random algorithm. The model is then reduced (pruned) to a more parsimonious form by eliminating nonsignificant partitions of the data (Venables and Ripley 1994).

Fig. 1. Predictor variables used in multiple regression and regression tree models to explain bitter cherry distribution. All variables were categorical except aspect, which was cosine transformed, and elevation, which was treated as a continuous variable. Vertical lines represent 10th and 90th percentiles, boxes enclose 80% of the data, horizontal lines inside boxes indicate median values, and short horizontal lines indicate mean values.

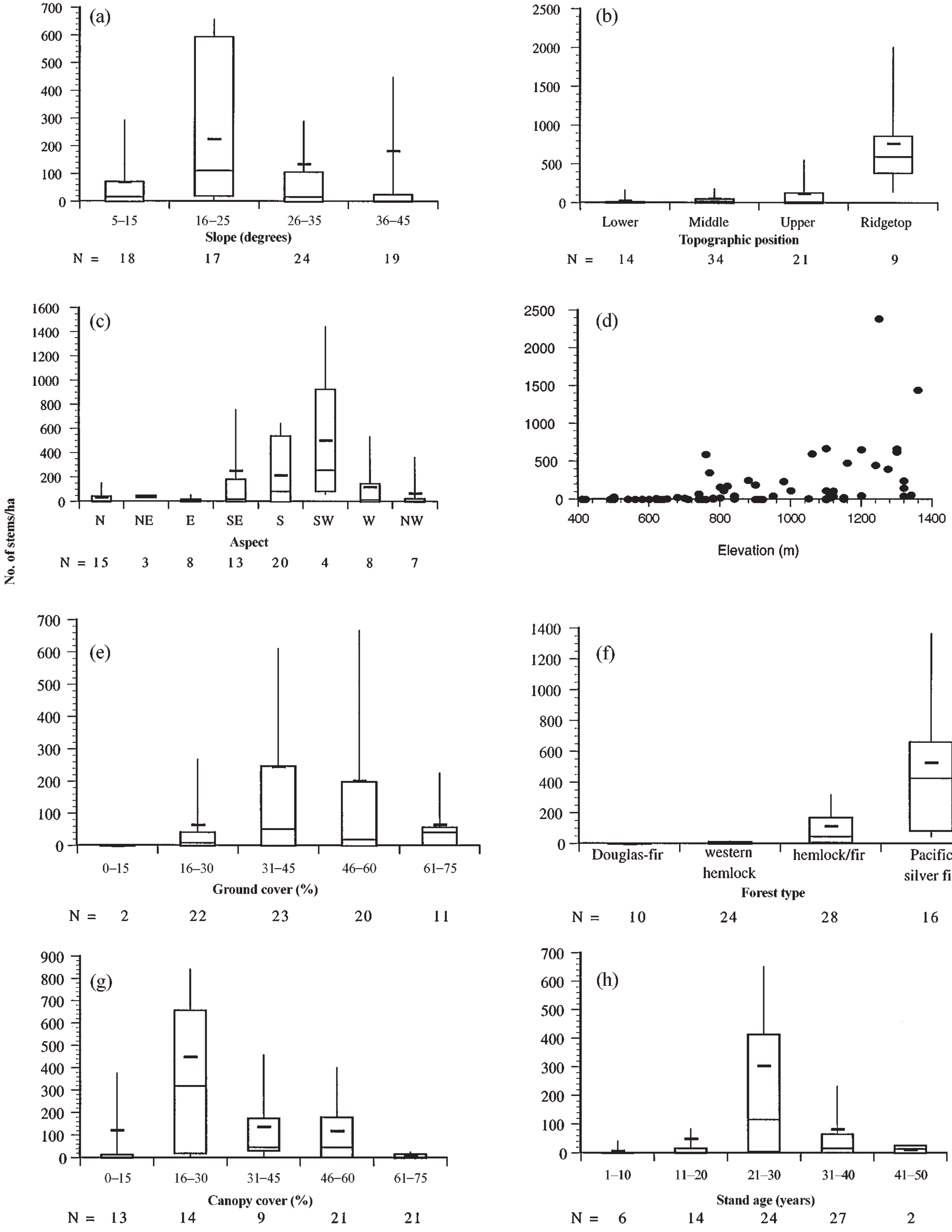
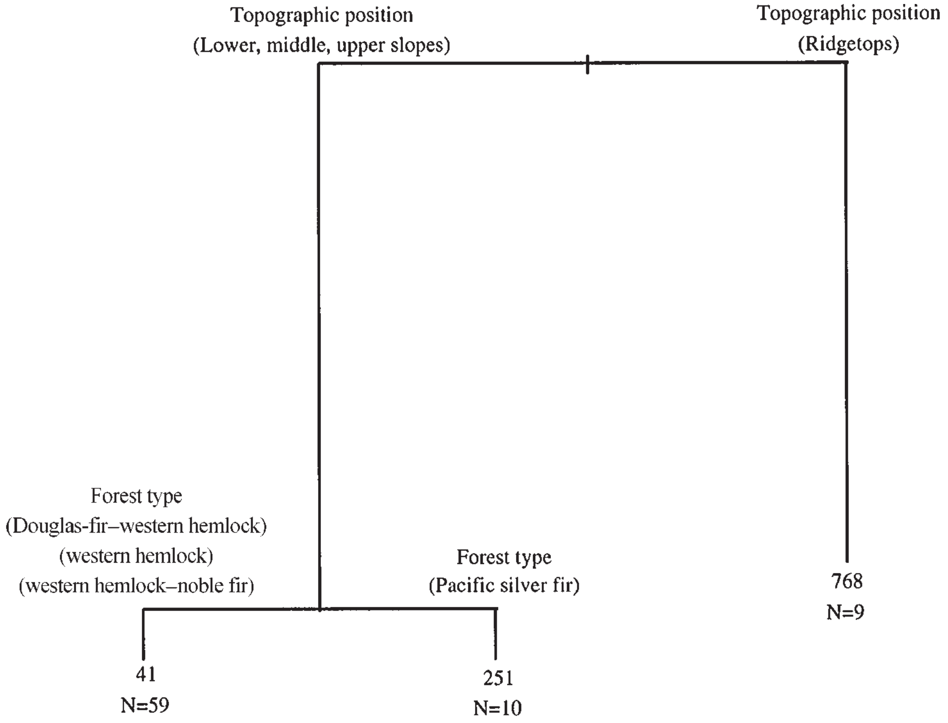


Fig. 2. Significant predictor variables describing bitter cherry distribution in the H.J. Andrews Experimental Forest. Values at the terminal nodes represent the mean number of bitter cherry stems per hectare and sample sizes.



Successional patterns

Permanent plot data and historical records were used to quantify bitter cherry patterns of abundance through time. This began after completion of logging in 1966 (year 0) and continued every 1–4 years through 1994 (year 28). Permanent 2 × 2 m plots were used to measure the canopy cover of all vascular plants less than 6 m tall, including bitter cherry (Dyrness 1973, Halpern 1989). In 1980 (year 14), 250-m^2 circular plots were established to track the dynamics (growth and mortality) of all trees taller than breast height (1.37 m). Each circular plot was centered on each of the original 4-m^2 plots. Remeasurements occurred in 1984, 1988, 1991, and 1995 (year 18, 22, 25, and 29). Stems that had reached breast height since the previous sampling year were recorded as recruitment and trees that had died recorded as mortality. Frequency (constancy among sample plots) was calculated for both the 4-m^2 cover plots and the 250-m^2 tree plots.

To estimate the longevity of bitter cherry, historical records from permanent plots throughout the Northwest (Williamson 1963) were summarized.

Seed sampling

To determine if bitter cherry maintains a viable seed bank, endocarps (the hard protective coating around the seed) buried in the soil were collected from three types of sites: 58 soil samples in three stands with high bitter cherry stem density (>600 stems/ha), 34 samples in three stands with low stem density (<70 stems/ha), and 34 samples in a ca. 100-year-old stand with only decayed bitter cherry stems visible on the ground. Soil samples were collected at 10-m intervals on opposite sides of line transects located at random bearings. The litter layer and mineral soil to ca. 20 cm deep were collected through a 400-cm^2 frame and sieved on site through a 3.2-mm metal screen. Endocarps were classified into three categories: intact empty endocarps, intact endocarps with a viable seed, and endocarps with a single hole indicative of seed predation. All intact endocarps were tested for viability using a float test (Marks 1974). Intact endocarps that floated were empty, and those that sank contained a viable seed. All endocarps that sank were cracked open to confirm the presence of an intact, healthy seed.

To quantify the spatial distribution of the seed bank relative to live trees at the high and low stem density sites, the distance to the nearest live stem was measured for each sample.

Results

Distribution

Most bitter cherry trees in the HJA were found in the Pacific silver fir zone on south aspects and ridgetops (Fig. 1). In the regression model (R^2 = 0.67), forest type and aspect were the only significant variables. Residual analysis of the model did not reveal any violations of regression assumptions.

In the regression tree reduced to its most parsimonious form, only topographic position and forest type were significant (Fig. 2). Sites on ridgetops had the highest mean density (768 stems/ha). The second partition of the data was based on forest type with highest mean density (251 stems/ha) on sites in the Pacific silver fir zone.

Succession

Bitter cherry slowly colonized Watershed 1 during the first decade after disturbance, rapidly increased through the second decade, and began to decline by the end of the third decade. Bitter cherry was measured in the first growing season after logging on 1.5% of the 4-m^2 plots, but constancy and cover remained low (<10% and <1% respectively) until both rapidly increased between years 14 and 24 (Fig. 3). By

Fig. 3. Constancy (frequency among sample plots) on 250-m^2 plots (+) and 4-m^2 plots (△), and total percent cover on 4-m^2 plots (●) from 1966 (year 0) to 1995 (year 29). Year 0 represents the first sampling after logging and year 1 the first sampling after slash burning. Cover values are mean ± SE. Measurements on the 250-m^2 plots began in year 14.

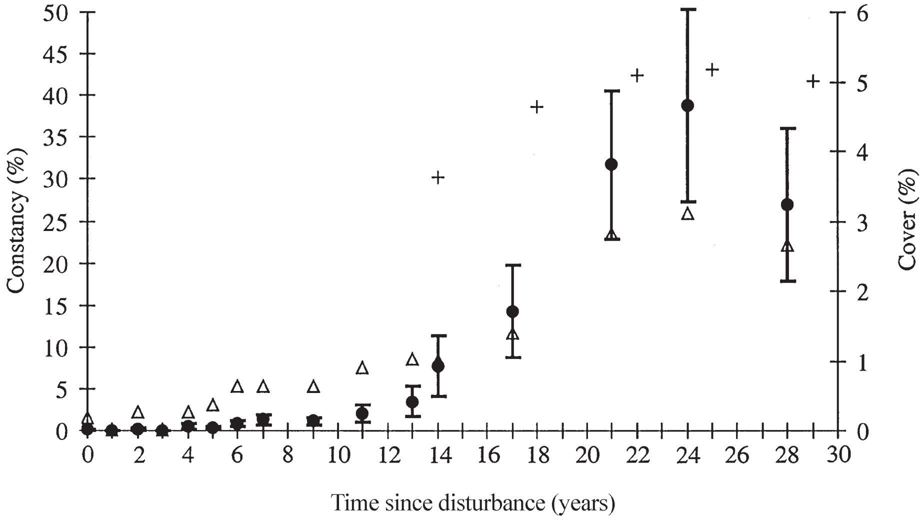
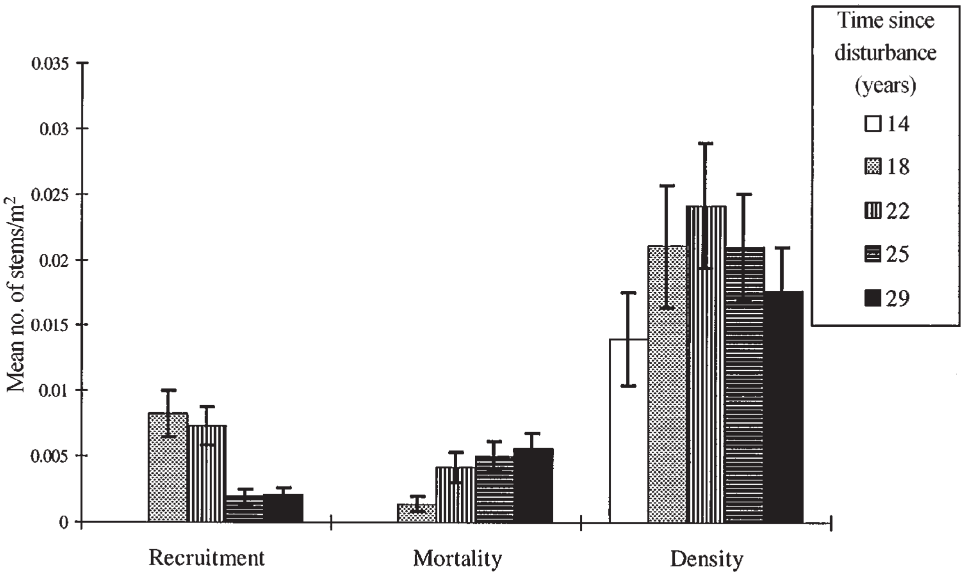


Fig. 4. Summary of bitter cherry recruitment, mortality, and density from 1980 (year 14) to 1995 (year 29) for all 250-m^2 plots. Note that time steps are not annual. Error bars are ± 1 SE.



year 28, both measures had declined from maxima in year 24. Constancy among the larger (250-m^2) circular plots followed a similar pattern, increasing to a maximum in year 25, and subsequently declining in year 29 (Fig. 3).

Stem density also increased through the second decade and reached a maximum in the third decade after disturbance. On Watershed 1, density reached a maximum in year 22 (Fig. 4) and in clearcuts across the HJA, most bitter cherry were found in stands 21–30 years old (Fig. 1*h*). Recruitment generally declined and mortality increased through the sampling period on Watershed 1 (Fig. 4).

Bitter cherry does not persist in forest stands past about 100 years after disturbance. Historical data compiled from 10 permanent plot studies in Washington and Oregon show bitter cherry was last observed between 63 and 109 years after disturbance (Williamson 1963; S. Acker, unpublished data).

Seed bank characteristics

Bitter cherry may maintain a viable seed bank. Intact endocarps and viable seeds were found in the soil at all sites (Table 1). Seeds in the soil were found only a short distance from live bitter cherry stems (Fig. 5). Most (98 and 87%) viable seeds were found within 3 m of the nearest stem at the high density and low density sites, respectively.

Decreases in the seed bank occur with time. Samples from the 100-year-old stand with no live bitter cherry had fewer viable seeds and more predated seeds than samples from stands with live stems (Table 1).

Fig. 5. Spatial distribution of bitter cherry intact empty endocarps (○) and viable seeds (●) relative to live stems (N = 80).

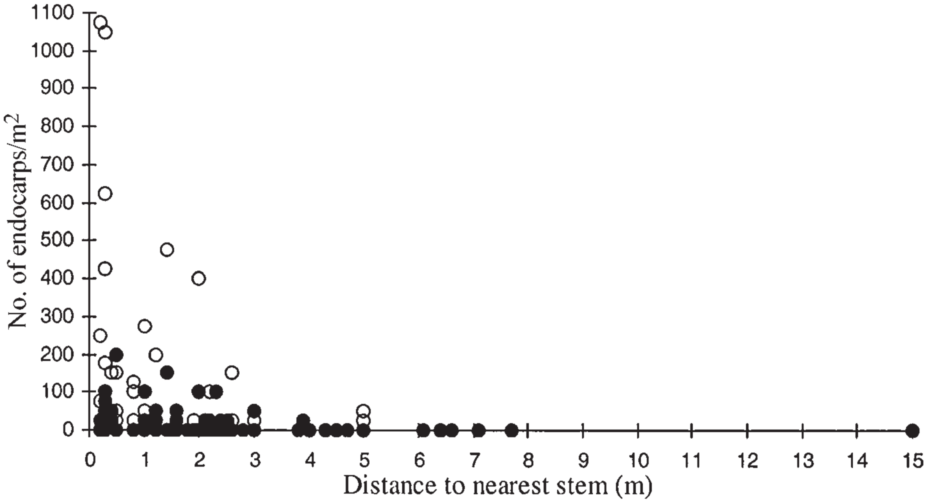


Table 1. Number of bitter cherry empty endocarps, viable seeds, and predated seeds/m^2.

Bitter cherry stem density	Empty endocarps	*N*	Viable seeds	*N*	Predated seeds	*N*
High (>600 stems/ha)	65.8±17.6	46	25.0±6.4	46	32.8±7.6	58
Low (<70 stems/ha)	112.5±45.9	34	11.0±4.1	34	7.4±3.4	34
None (dead)	81.6±22.5	34	9.6±2.8	34	47.8±15.7	34
Total	84.4±16.7	114	16.0±3.0	114	30.0±5.7	126

Note: Values are mean ± SE. *N*, Number of soil samples.

Discussion

Existing literature describes bitter cherry as an early successional (e.g., Sudworth 1908; Taylor and Taylor 1981; Pojar and Mackinnon 1994) and obligate seed bank species (Morgan and Neuenschwander 1988), but its successional dynamics and the importance of the seed bank strategy have not been thoroughly examined. Because bitter cherry establishment was delayed for at least a decade after disturbance, we inferred that regeneration from a seed bank has not been an important mechanism by which current populations responded to disturbance. If clearcuts in the HJA had contained a large seed bank prior to disturbance, relatively high numbers of seedlings and saplings would have germinated in the first few years after disturbance in response to changes in light, temperature, or moisture. Halpern (1989) also noted bitter cherry as a slow colonizer on Watershed 1 and suggested that animal dispersal, rather than growth from a seed bank, explained this response.

We did find viable seeds in the soil at densities that were within the range of those previously described (Kramer and Johnson 1987; Morgan and Neuenschwander 1988), but based on the patterns of successional dynamics we observed and the possible recent origins of seeds found in the soil, we find it difficult to agree with a designation of bitter cherry as an obligate seed bank species. Several alternative explanations are possible for the existence of viable seeds in the soil. First, although the float test to determine seed viability has been used successfully in the past (Marks 1974), it may overestimate actual viability. Second, seeds we collected may have been deposited by multiple generations of trees that have reached reproductive age since the first colonists arrived. This may explain the strong increases in stem density in the 21- to 30-year age-class. Finally, *Prunus* fruits are well adapted to animal consumption and dispersal, which may have contributed viable seeds to the soil.

However, we did find viable seeds at a site where, based on the age of the stand, the life span of bitter cherry and the appearance of decayed stems on the ground, the last cherry tree had probably died several decades ago. More recent animal deposition of these seeds is again possible but unlikely. Therefore, despite the several possible origins of the viable seeds we found, it does appear that bitter cherry is able to maintain a viable seed bank, perhaps for several decades.

For the seed bank strategy to be successful, however, disturbance intervals must not exceed the longevity of the seed bank. Optimal return intervals for the regeneration of bitter cherry from a seed bank are probably much shorter than the historical disturbance interval at the HJA. Although the HJA has experienced limited low-severity fires within the last 150 years, late-successional forests had existed for several centuries before logging (Teensma 1987). It is therefore unlikely that any significant bitter cherry seed bank existed when the stands we measured were logged, which is consistent with the delayed response of bitter cherry regeneration we observed.

Support for this idea comes from research on the closely related pin cherry (*Prunus pensylvanica* L.). Pin cherry in the Northeast requires major disturbances within a maximum interval of 125 years for effective regeneration from a seed bank (Peterson and Carson 1996). High-density pin cherry stands that arise from a seed bank (sensu Marks 1974) are the product of frequent disturbances, which have included logging in the early 1900s, a hurricane in 1938, and logging again in the 1970s (Hibbs 1983; Foster 1988; Peterson and Carson 1996). With each successive disturbance, more seeds are produced and accumulate in the soil. In forests that have not been subject to frequent disturbances, pin cherry has a small seed bank, and consequently pin cherry regeneration is limited (Foster 1988; Merrens and Peart 1992; Peterson and Carson 1996).

This requirement for frequent disturbance may explain why bitter cherry did not regenerate from a seed bank in the HJA despite its ability to store viable seeds in the soil and may also influence its distribution patterns. The concentration of bitter cherry on ridgetops and south aspects may be a reflection of relatively high disturbance frequencies in these areas (Romme and Knight 1981; Teensma 1987), allowing bitter cherry to accumulate a seed bank. (The concentration of bitter cherry on ridgetops may also be an artifact of covariation between topographic position and forest type; of nine ridgetop sites, six were in the Pacific silver fir zone, where the highest densities of bitter cherry were found.) Mueggler (1965) also found bitter cherry positively associated with south aspects, and dense bitter cherry stands at high elevations have been noted (Jones 1936; Taylor and Taylor 1981). However, our results contrast with some published descriptions of the species as preferring moist lowland forests or streambanks (e.g., Pojar and Mackinnon 1994).

Although our conclusions may be limited by the use of a single watershed and the difficulties inherent in an observational study, considering the role of a seed bank may help to predict the future importance of bitter cherry in the Pacific Northwest. If infrequent disturbances are in fact a limiting factor for successful utilization of the seed bank strategy, increased disturbance may lead to a greater role in succession for bitter cherry, similar to pin cherry in the Northeast. Beginning in the 1950s, clearcutting has been the primary disturbance on the HJA and surrounding national forests, creating large areas of early successional habitat. As second-growth stands are harvested again, bitter cherry may be able to regenerate from seeds stored in the soil since the first disturbance. At a stand scale, frequent disturbances may stimulate compounding accumulations of seeds and high bitter cherry density. At a landscape or regional scale, frequently disturbed habitat may function as a source for bitter cherry colonization of newly disturbed areas.

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References

Beers, R.W., Dress, P.E., and Wensel, L.C. 1966. Aspect transformation in site productivity research. J. For. **64**: 691–692.

Bierlmaier, F.A., and McKee, A. 1989. Climatic summaries and documentation for the primary meteorological station, H.J. Andrews Experimental Forest, 1972 to 1984. USDA For. Serv. Gen. Tech. Rep. No. PNW-242.

Breiman, L., Friedman, J.H., Olshen, R., and Stone, C.J. 1984. Classification and regression trees. Wadsworth International Group, Belmont, Calif.

Chambers, J.M., and Hastie, T.J. 1992. Statistical models in S. Wadsworth & Brooks/Cole Advance Books & Software, Pacific Grove, Calif.

Cronemiller, F. P. 1959. The life history of deerbrush: a fire type. J. Range Manage. **12**: 21–25.

Dyrness, C.T. 1973. Early stages of plant succession following logging and slash burning in the western Cascades of Oregon. Ecology, **54**: 57–68.

Dyrness, C.T., Franklin, J.F., and Zobel, D. 1971. Identification and characterization of forest communities and habitat types in and adjacent to the H.J. Andrews Experimental Forest. Coniferous For. Biome Internal Rep. No. 7. University of Washington, Seattle, Wash. pp. 55–62.

Dyrness, C.T., Franklin, J.F., and Moir, W.H. 1976. A preliminary classification of forest communities in the central portion of the western Cascades in Oregon. Bull. No. 4. Coniferous Forest Biome, United States – International Biological Program, Seattle, Wash.

Foster, D.R. 1988. Disturbance history, community organization and vegetation dynamics of the old-growth Pisgah forest, southwestern New Hampshire, U.S.A. J. Ecol. **76**: 105–134.

Franklin, J.F., and Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oreg.

Gratkowski, H. 1974. Origin of mountain whitethorn brushfields on burns and cuttings in Pacific Northwest forests. West. Soc. Weed Sci. Proc. **27**: 5–8.

Halpern, C.B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology, **70**: 704–720.

Hibbs, D.E. 1983. Forty years of forest succession in central New England. Ecology, **64**: 1394–1401.

Jones, G.N. 1936. A botanical survey of the Olympic Peninsula. Univ. Wash. Publ. Biol. Vol. 5. University of Washington Press, Seattle, Wash.

Kramer, N.B., and Johnson, F.D. 1987. Mature forest seed banks of three habitat types in central Idaho. Can. J. Bot. **65**: 1961–1966.

Livingston, R.B., and Allessio, M.L. 1968. Buried viable seed in successional field and forest stands, Harvard Forest, Massachusetts. Bull. Torrey Bot. Club, **95**: 58–69.

Marks, P.L. 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. Ecol. Monogr. **44**: 73–88.

Merrens, E.J., and Peart, D.R. 1992. Effects of hurricane damage on individual growth and stand structure in a hardwood forest in New Hampshire, USA. J. Ecol. **80**: 787–795.

Mladenoff, D.J. 1990. The relationship of the soil seed bank and understory vegetation in old-growth northern hardwood – hemlock treefall gaps. Can.. J. Bot. **68**: 2714–2721.

Moore, J.M., and Wein, R.W. 1977. Viable seed populations by soil depth and potential site recolonization after disturbance. Can. J. Bot. **55**: 2408–2412.

Morgan, P., and Neuenschwander, L.F. 1988. Seed-bank contributions to regeneration of shrub species after clear-cutting and burning. Can. J. Bot. **66**: 169–172.

Mueggler, W.F. 1965. Ecology of seral shrub communities in the cedar–hemlock zone of northern Idaho. Ecol. Monogr. **35**: 165–185.

Mueller-Dombois, D., and Ellenberg, H. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York.

Neter, J., Wasserman, W., and Kutner, M.H. 1990. Applied linear statistical models: regression, analysis of variance, and experimental designs. Irwin, Burr Ridge, Ill.

Olmstead, N.W., and Curtis, J.D. 1947. Seeds of the forest floor. Ecology, **28**: 49–52.

Oosting, H.J., and Humphreys, M.E. 1940. Buried viable seeds in a successional series of old field and forest soils. Bull. Torrey Bot. Club, **67**: 253–273.

Orme, M.L., and Leege, T.A. 1974. Emergence and survival of redstem (*Ceanothus sanguineus*) following prescribed burning. Proc. Tall Timbers Fire Ecol. Conf. **14**: 391–420.

Peterson, C.J., and Carson. W.P. 1996. Generalizing forest regeneration models: the dependence of propagule availability on disturbance history and stand size. Can. J. For. Res. **26**: 45–52.

Pojar, J., and Mackinnon, A. 1994. Plants of the Pacific Northwest coast. Lone Pine Publishing, Vancouver, B.C.

Romme, W.H., and Knight, D. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. Ecology, **62**: 319–326.

Rothacher, J., Dyrness, C.T., and Fredriksen, R.L. 1967. Hydrologic and related characteristics of three small watersheds in the Oregon Cascades. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oreg.

Spies, T.A., Ripple W.J., and Bradshaw, G.A. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecol. Appl. **4**: 555–568.

Sudworth, G.B. 1908. Forest trees of the Pacific Slope. Government Printing Office, Washington, D.C.

Swanson, F.J., and James, M.E. 1975. Geology and geomorphology of the H.J. Andrews Experimental Forest, western Cascades, Oregon. USDA For. Serv. Pac. Northwest For. Range Exp. Stn. Res. Pap. No. PNW-188.

Taylor, R.L., and Taylor, S. 1981. *Prunus emarginata* in British Columbia. Davidsonia, **12**(3): 78–83.

Teensma, P. 1987. Fire history and fire regimes of the central western cascades of Oregon. Ph.D. dissertation, University of Oregon, Eugene, Oreg.

Venables, W.N., and Ripley, B.D. 1994. Modern applied statistics with S-Plus. Springer-Verlag, New York.

Williamson, R.J. 1963. Growth and yield records from well-stocked stands of Douglas-fir. USDA For. Serv. Pac. Northwest For. Range Exp. Stn. Res. Pap. No. PNW-4.

Zar, J.H. 1984. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J.