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Structure, Composition, and Reproductive Behavior of Terrace Forests, South Fork Hoh River, Olympic National Park

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ABSTRACT

Mature forests of Picea sitchensis and Tsuga heterophylla varied with terrace level. Upper terraces had denser stands, greater numbers of Tsuga, and understories of Vaccinium, ferns, and mosses. Lower terraces had open stands with understories of Acer circinatum and grasses. Tree reproduction occurred primarily on down logs. Less than 1 percent occurred on ground humus. Picea reproduction numbers and survival rates were superior to Tsuga. Tsuga reproduction may have exceeded that of Picea earlier. Both similarities and differences exist with Fonda's Hoh River model. Picea was apparently climax in these terrace forests in contrast to other coastal types.

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Franklin (in this report) has described the relationships of the vegetation studies to the other portions of the South Fork Project. Plant community analyses in the South Fork were directed toward collecting baseline vegetation data in a manner that would facilitate their interpretation relative to topographic position and proximity to aquatic habitats. Previous studies by members of the research team had shown the importance of woody debris in mediating erosional processes (Swanson 1980). Information was sought to examine these interactions in a coastal ecosystem and the results are presented by Swanson and Lienkaemper in this report.

From research in the main valley of the Hoh River, Fonda (1974) proposed a successional model for river terrace forests that interpreted successively higher terraces as a series of seral stages tending toward a climax forest of Tsuga heterophylla. Terrace formation occurs by meandering of the river and periodic flooding. The wide valley floor of the South Fork of the Hoh River with its extensive terraces seemed an appropriate place to test the generality of Fonda's (1974) model.

More knowledge of the successional roles of Picea sitchensis and Tsuga heterophylla was needed to further evaluate the above model. In mature forests of the coastal fog belt (Franklin and Dyrness 1973) and on alluvial terraces bordering the lower reaches of coastal rivers (Cordes 1972), the two species compete strongly for dominance. In some habitats P. sitchensis seems unable to co-exist indefinitely with T. heterophylla in the absence of disturbances because it is less shade tolerant (Fowells 1965). P. sitchensis succeeds Alnus rubra in alluvial terraces for some distance inland, becoming the dominant tree species (Cordes 1972, Fonda 1974). It may be more tolerant of seasonal flooding in these sites than T. heterophylla. As one of the major attractions of the Olympic National Park, the stability and successional fate of the terrace forests is of extreme interest. Therefore, regeneration behavior of P. sitchensis and T. heterophylla was a major part of the vegetation studies.

This paper discusses the vegetation of the South Fork terraces in terms of upper versus lower terrace stands, but the collation of our terms with those of the geomorphologists is critical. At least six terrace surfaces have been recognized in the study area (see Swanson and Lienkaemper in this report). Surfaces 1, 2, and 3 range from fresh gravel bars to low terraces with young A. rubra stands. Their surfaces 4, 5, and 6 are occupied by mature, conifer-dominated forests and are the locale of the studies reported here. Data from surfaces 5 and 6 are combined for our "upper terrace" values. Surface 4 is our "lower terrace." Although it is difficult to draw exact comparisons between the adjacent river valleys, our lower terrace is believed roughly equivalent to Fonda's (1974) first terraces, and our upper terrace is roughly equivalent to his second terrace.

METHODS

Two different vegetation sampling procedures were employed in this study to accommodate the diverse needs of the group (see Franklin in this report). Transects allowed us to examine the interactions between topographic position, vegetation, and aquatic habitats. A point-quarter sampling method was used at 50-m intervals on these transects. Herbaceous cover was estimated in eight microplots (20- x 50-cm) around each point. Shrub cover was estimated by line intercept along the transects.

The remainder of the vegetation sampling was conducted on the four large (1-ha) permanent plots (see Franklin in this report). Detailed sampling of down logs for dimensions and decay class is described by Lambert, in this report, who provided the basic data utilized here on log numbers and surface area.

Restricted random sampling was performed on each of the two terrace stands of the immature tree subpopulations (stem $\leq$ 8 m tall). Five major substrate types were sampled: ground duff and humus, tree stumps and uprooted tree bases ("root wads"), P. sitchensis logs, T. heterophylla logs, and logs unidentifiable as to species. The three log substrates were further subdivided by a decay class scheme (see Lambert in this report). A logarithmic height classification system was used in tallying seedlings and saplings in which the height range of each taller class is doubled: e.g., (1) $<$ 0.125 m; (2) 0.125 - 0.25 m; (3) 0.25 - 0.5 m, etc. This was done to achieve a greater resolution in smaller size classes.

Biomass estimates were made from data collected on the four permanent plots using allometric equations developed by the Coniferous Forest Biome (Gholz et al. 1979). Heights of selected trees were measured on the permanent plots. Ages of overstory dominants were determined by increment cores taken along the transects.

RESULTS

Structure and Composition

Forests on the valley floor of the South Fork of the Hoh River were dominated by P. sitchensis and T. heterophylla except for recently created, relatively narrow terraces along the main river channel, which were dominated by A. rubra. Much of the valley floor of the South Fork consists of two relatively distinct terraces, however, and most of the following discussion is a comparison of these upper and lower terraces. Although there are similarities, the data from the transects and permanent plots are evidence that different terrace levels were occupied by stands that differ substantially in structure and composition.

Both upper and lower terraces had similar ages and heights of the overstory Picea and Tsuga. Mean and maximum ages at 1.5 m above ground were 220 and 266 years on the upper and 205 and 258 years on the lower terrace. The tree strata on both terraces consisted of a tall tree layer of P. sitchensis 75 to 80 m in height and a medium tree layer of T. heterophylla and P. sitchensis of 45 to 55 m. Maximum heights measured on both terraces exceeded 85 m. Mean heights and ages were slightly greater on the upper terrace, but sampling was insufficient for a test of significance.

Table 1--Mean densities, basal areas, and diameters by species for upper and lower terrace forests of the South Fork of the Hoh River

Species[1]	Density		Basal area		Mean diameter	
	Upper	Lower	Upper	Lower	Upper	Lower
	Number per hectare		Square meter per hectare		Centimeters	
PISI	57.8	33.1	61.9	52.8	90.4	118.4
TSHE	79.9	24.7	15.8	10.3	45.8	64.9
THPL	2.1	[2]0.3	1.0	[2]0.8	73.0	[2]176
PSME	1.7	--	2.9	--	114.0	--
ALRU	[2]0.3	5.3	[2]0.03	1.9	[2]28.0	64.9
ACMA	--	0.7	--	0.4	--	84.0
ABAM	[2]0.3	--	[2]0.1	--	[2]51.0	--
All species	142	64	81.8	66.3	65.6	93.3

[1] Species are: PISI - Picea sitchensis, TSHE - Tsuga heterophylla, THPL - Thuja plicata, PSME - Pseudotsuga menziesii, ALRU - Alnus rubra, ACMA - Acer macrophyllum, and ABAM - Abies amabilis.

[2] Only one individual in the sample.

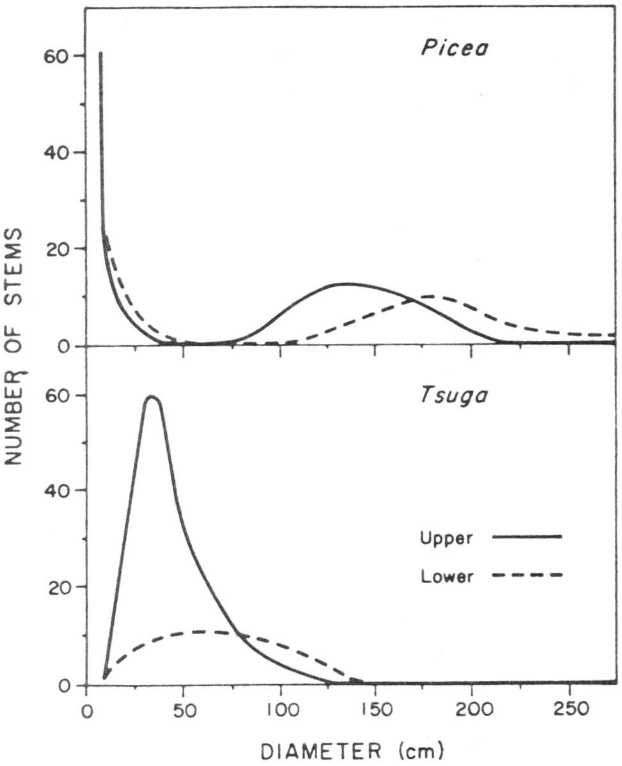

Figure 1.--Diameter distributions for all Picea sitchensis and Tsuga heterophylla sampled which were over 5 cm in diameter on upper and lower terraces.

Upper and lower terrace stands differed substantially in several structural and compositional features (table 1 and fig. 1). Total density and basal area were greater in upper terrace than lower terrace stands: 142 vs. 64 stems/ha and 81.8 vs. 66.3 m^2/ha. Mean diameters, on the other hand, were greater on the lower than the upper terrace. P. sitchensis averaged 118-cm d.b.h. on the lower and 90-cm d.b.h. on the upper terrace, while T. heterophylla averaged 65- and 46-cm d.b.h. respectively. The larger diameters on the lower terraces may have been due to wider spacing which results in reduced competition or to better site conditions or both. Diameter distributions of P. sitchensis and T. heterophylla showed that, except for the smallest size class, P. sitchensis had peak densities at substantially larger size classes than T. heterophylla on both terraces (fig. 1). The bimodal nature of the P. sitchensis diameter distributions on both terraces should be noted. The implications of this distribution will be discussed later in the section on regeneration.

The biomass estimates in table 2 reflect some of the structural variation encountered in upper and lower terrace stands. Total biomass was measured in metric tonnes per hectare (t/ha) and averaged more in the upper terrace permanent plots than in the lower terrace. Considerable variation existed, however, in the biomass of P. sitchensis in the upper terrace plots and in T. heterophylla in the lower terrace plots. Total biomass was quite high on both terraces for 200- to 250-year-old stands, indicating the productive nature of the Picea-Tsuga forests.

Composition differs dramatically between upper and lower terrace forests. T. heterophylla was of much greater importance in upper terrace stands as shown by the density and basal area values (table 1). Minor tree species such as Pseudotsuga menziesii and Abies amabilis seemed confined to upper terraces. Alnus rubra was much more important on the lower terraces (tables 1 and 2).

Understory composition also differed between the two terraces (table 3). Composition of the shrub layer shifted from Acer circinatum-dominated to Vaccinium-dominated. Cover of Acer circinatum dropped from 28.2 to 2.4 percent as one went from lower to upper terrace stands, while Vaccinium cover went from 0.6 to 10.8 percent. Total shrub cover was twice as great on the lower terrace. The herbaceous layer of lower terrace stands was dominated by grasses and forbs with 25.4- and 37.3-percent cover, respectively. As with Acer, grass cover dropped dramatically in upper terrace stands. Mosses and ferns became much more important in the upper terrace forests. Total cover of forbs decreased slightly in upper terrace forests. Species composition of the forbs was quite similar on both terraces.

Table 2--Biomass estimates (metric tonnes per hectare) for four permanent 1-ha plots established September 1978 in upper and lower terrace forests of the South Fork of the Hoh River, Olympic National Park. Calculated for stems ≥ 15-cm d.b.h.

	Bole and bark		Branches		Foliage[2]		Total	
Species[1]	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower
PISI	442.4	428.4	50.7	51.7	4.2	4.0	497.3	484.1
	740.5	446.8	86.2	53.4	6.9	4.2	833.6	504.3
TSHE	110.6	36.4	33.6	12.8	6.3	2.1	150.4	53.3
	62.7	154.6	18.3	56.8	3.6	8.1	84.6	219.4
THPL	2.6	10.8	0.5	1.9	0.2	0.7	3.3	13.4
	0.3	--	0.2	--	0.1	--	1.1	--
PSME	17.2	--	0.8	--	0.2	--	18.3	--
	22.9	--	1.1	--	0.3	--	24.2	--
ALRU	--	5.0	--	0.6	--	0.03	--	5.6
	—	4.1	--	0.5	—	0.02	--	4.6
Total	572.8	482.6	85.6	67.0	10.9	6.9	669.3	556.4
	829.7	605.4	106.1	110.6	11.1	12.3	946.8	728.3
$\bar{x}$	701.2	544.0	95.8	88.8	11.0	9.6	808.0	642.4
s_d	181.7	86.8	14.5	30.8	0.1	3.8	196.2	121.6

[1] Species are: PISI = *Picea sitchensis*, TSHE = *Tsuga heterophylla*, THPL = *Thuja plicata*, PSME = *Pseudotsuga menziesii*, and ALRU = *Alnus rubra*.

[2] Foliar biomass estimates for *Picea* are conservative because the equations used (Gholz et al. 1979) are partially based on wind-trimmed trees.

Table 3--Mean composition of shrub and herbaceous layers of forest communities on the upper and lower terraces of the South Fork of the Hoh River

	Shrub layer[1], % Cover					Herbaceous layer, % Cover			
	ACCI	VAsp	RUSP	MEFE	∑	Forbes	Grasses	Mosses	Ferns
Upper terrace	2.4	10.8	1.9	.03	15.1	29.8	4.8	64.3	13.5
Lower terrace	28.2	0.6	1.8	0.0	30.6	37.3	25.4	42.4	6.8

[1] Shrub species abbreviations are: ACCI = *Acer circinatum*, VAsp = *Vaccinium* species, RUSP = *Rubus spectabilis*, and MEFE = *Menziesia ferruginea*.

Table 4--*Picea sitchensis* and Tsuga *heterophylla* subpopulation density (stems $\leq$ 8 m tall/m^2) on the 5 major substrate types and 4 major log decay classes in the upper and lower terrace forests, South Fork Hoh River, Olympic National Park

Substrate type and log decay class	Upper terrace *Picea*	Upper terrace *Tsuga*	Lower terrace *Picea*	Lower terrace *Tsuga*
Substrate type:				
Picea logs	36.0	15.3	19.3	6.6
Tsuga logs	29.9	9.6	11.3	4.3
Unknown logs	30.0	7.5	11.5	5.1
Stumps and root wads	5.1	1.6	7.7	2.9
Ground humus	0.08	0.01	0.08	0.01
Log decay class:				
2. Early	24.8	15.5	8.3	2.0
3. Middle	38.5	10.7	21.7	7.7
4. Late	28.6	9.2	11.9	5.4
5. Very late	28.2	8.2	11.9	4.7

One interesting aspect of species composition concerned the naturalized Eurasian weeds. These exotic species were confined almost entirely to lower terrace stands and recently formed terraces and gravel bars. The only exotic species encountered in the upper terraces were *Agrostis alba* and *Prunella vulgaris*, and these were rare. The other exotic species--*Poa trivialis*, *Ranunculus repens*, *Rumex acetosella*, *Rumex crispus*, *Trifolium repens*, and *Lactuca serriola*--seem restricted to the lower terraces. *Agrostis alba*, *Poa trivialis*, and *Ranunculus repens* were important components of the lower terrace herbaceous layer with covers frequently exceeding 20 percent. The other species tended to be locally important or rare. Fonda's (1974) data show these Eurasian weeds similarly distributed on the terraces in the main stem of the Hoh River. Historically, traffic of both humans and livestock has been heavier in the more open lower terraces. These factors and the more frequent disturbance by flooding on the lower terraces were probably the reasons for the current distribution of exotics.

Forest Tree Reproduction

Regeneration on Different Substrates

The density of seedlings and saplings less than 8 m tall growing on the five major substrate types on the two terraces is given in table 4. Both *P. sitchensis* and *T. heterophylla* obviously had difficulty establishing on ground humus in the two terrace stands. Down logs are a much more favorable site for establishment. *P. sitchensis* logs are better recruitment sites than *T. heterophylla* logs for both tree species. This difference is confirmed by chi-square tests and also has been observed by Minore (1972).

Total recruitment densities of *P. sitchensis* were higher than those for *T. heterophylla* on all five substrates in both terrace stands. Environmental conditions during the life span of these seedlings and saplings have clearly favored *P. sitchensis* over *T. heterophylla*.

Regeneration on Different Log Decay Classes

Densities of seedlings and saplings on four different log decay classes also are tabulated in table 4. Both terraces lacked sufficient logs in class 1 to provide good tree seedling density estimates. *P. sitchensis* density was highest on class 3 logs on both terraces. The maximum density of *T. heterophylla* regeneration, however, was on class 2 logs in the upper terrace stands and class 3 logs in the lower terrace stands.

Chi-square tests support two conclusions: (1) tree recruitment potentials of fallen logs in the study area change significantly with decomposition stage and (2) the off-log environments of the two terraces exert a strong influence on the recruitment potential of different log decay classes. Seedling and sapling density is almost always greater on the upper than lower terrace for a given substrate type and species.

Total Regeneration

The data on densities on different substrates and decay classes reveal much about the behavior at the two tree species but do not show regeneration in the two terrace stands. Total density per hectare is the product of the above densities and the amount of surface area per hectare occupied by the different substrate types and decay classes. These calculations show *P. sitchensis* regeneration was approximately three times more abundant than *T. heterophylla* in both upper and lower terrace stands (table 5).

The importance of logs as a recruitment site is dramatically shown in table 5. Logs provided 96 and 88 percent of the *P. sitchensis* recruitment on the upper and lower terraces, respectively. Proportions of *T. heterophylla* were 97 and 93 percent. Class 3 logs are obviously of special importance (table 5). On a per hectare basis, they supported the largest number of seedlings and saplings less than 8 m tall for both species on both terraces.

Survivorship

Total densities (table 5) are interesting but do not reveal differences between species in abundance of different size classes. The abundance of *P. sitchensis* might be largely restricted to the smallest size classes, *T. heterophylla* to the largest, which would have vastly different implications for successional trends. Abundance data are presented in figure 2 as height-based survivorship curves for the two species on the two terraces. The regeneration sampling provided data for the first seven height classes, and the transect and permanent plot samples provided data for larger height classes.

Table 5--Calculated densities (stems ≤ 8 m tall) of Picea sitchensis and Tsuga heterophylla (ha^{-1}) on 5 major substrate types and 4 major log decay classes in the upper and lower terrace forests, South Fork Hoh River, Olympic National Park

Substrate type and log decay class	Upper terrace		Lower terrace	
	Picea	Tsuga	Picea	Tsuga
Substrate type:				
Picea logs	14,500	6,170	5,810	1,980
Tsuga logs	15,300	4,910	2,420	930
Unknown logs	4,920	1,230	600	260
Stumps and root wads	550	170	440	160
Ground humus	700	90	750	90
Total	35,970	12,570	10,020	3,420
Log decay class:				
2. Early	7,030	4,340	500	116
3. Middle	19,000	5,250	7,530	2,660
4. Late	7,800	2,500	1,730	780
5. Very late	820	170	80	30

The survivorship curves show P. sitchensis to be more abundant than T. heterophylla on both terrace forests for the first eight height classes (≤ 16 m tall) (fig. 2). The environmental conditions during the recent past have clearly favored P. sitchensis recruitment and survival. Such has not always been the case, however.

The survivorship curves for both terraces show an increase in T. heterophylla abundance in the larger size classes with a concomitant reduction of P. sitchensis (fig. 2). The diameter distributions shown in figure 1 revealed a greater abundance of T. heterophylla in the intermediate size classes, sandwiched between the peaks of the bimodal distribution of P. sitchensis. Hence, T. heterophylla regeneration was favored over P. sitchensis at some time in the past. The relative position of the survivorship curves for that period would have been reversed for both terraces, with T. heterophylla more abundant than P. sitchensis in the smaller size classes.

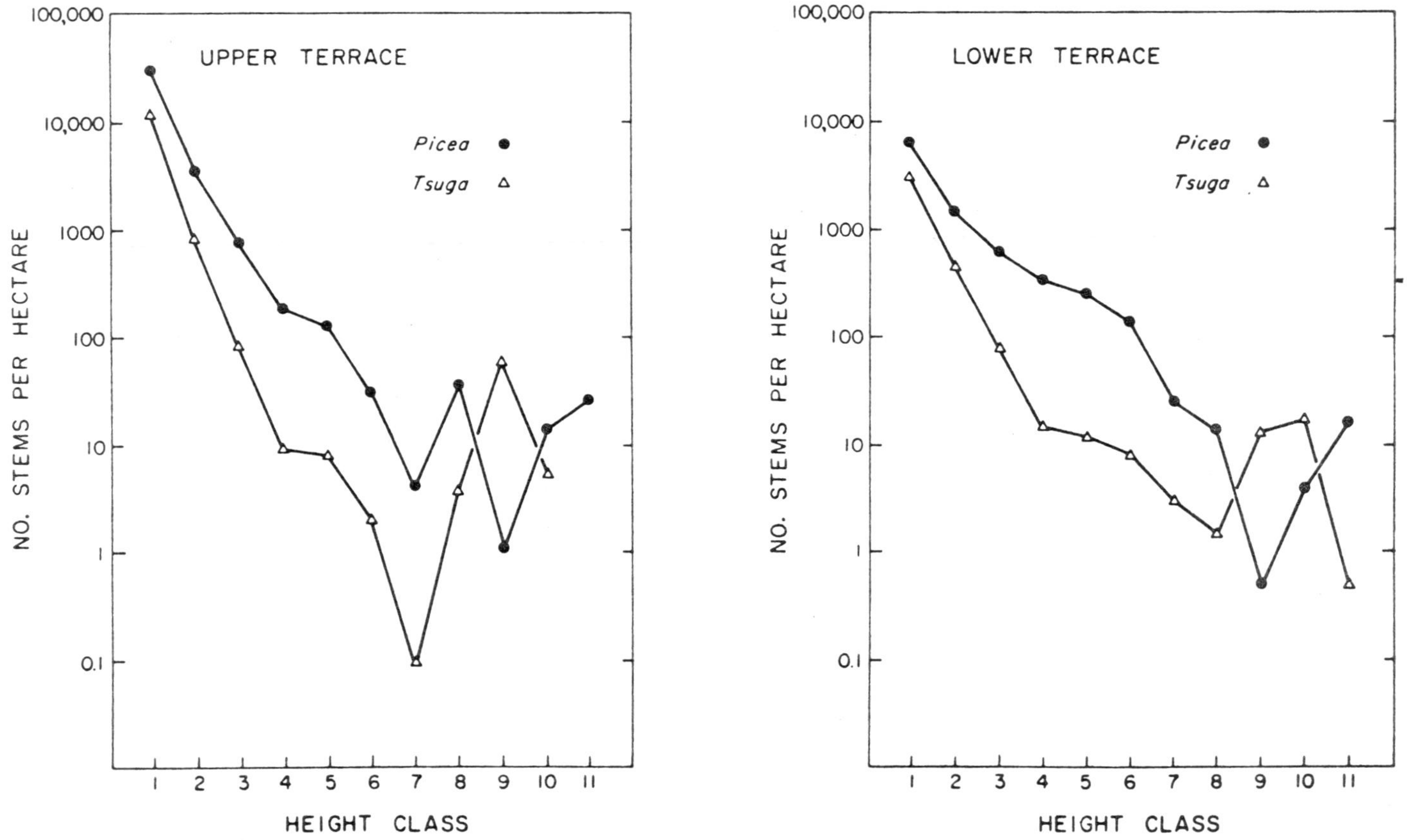

Figure 2.—Survivorship curves for Picea sitchensis and Tsuga heterophylla on lower and upper terrace forests in the South Fork of the Hoh River; each height class is twice as large as its predecessor (i.e., 1 = < 0.125 m, 2 = 0.125 to 0.25 m, 3 = 0.25 to 0.5 m, 4 = 0.5 to 1 m, 5 = 1 to 2 m, 6 = 2 to 4 m, 7 = 4 to 8 m, 8 = 8 to 16 m, 9 = 16 to 32 m, 10 = 32 to 64 m, and 11 = > 64 m tall).

DISCUSSION

The composition and structure of the terrace forests of the South Fork of the Hoh River have both similarities and differences with Fonda's (1974) terrace-based model developed for the main Hoh River drainage. The higher terraces supported increasing amounts of T. heterophylla in both the South Fork and the main Hoh River valleys. Grasses were an important component of the lower terraces in both systems; mosses increased in cover on the upper terraces. Forb cover remained relatively constant on all the terraces, and naturalized Eurasian weeds were confined almost entirely to the lower terraces in both valleys.

There were slight differences in the terrace forests between the two valleys, however. Alnus rubra is present in the lower terrace forests in the South Fork valley as well as on recent alluvium. The lower terrace forests in the South Fork appeared to be a much older version of Fonda's (1974) first terrace forest and lacked Populus trichocarpa. The upper terrace stands of the South Fork appeared to be intermediate to the second and third terrace forests of Fonda (1974). The upper and lower terrace stands of the South Fork had lower densities and higher basal areas than their analogs in the main Hoh River valley. Shrub cover was higher in the South Fork terraces with Acer circinatum much more abundant on the lower terraces and Vaccinium species more abundant on the upper terrace.

More important differences concerned the ages of the terrace forests and the role of P. sitchensis in the South Fork stands. In contrast to Fonda's (1974) model, the forests of the upper and lower terraces had dominants of about the same age and thus cannot be viewed as seral stages in a sequence of forest development. As shown by the survivorship curves, P. sitchensis regeneration was currently favored over T. heterophylla on both terraces. This is in contrast to what Fonda (1974) reports for even his third terrace forests which average two-thirds the basal area of our upper terrace stands, and thus should favor Picea by virtue of being less shaded.

Franklin and Dyrness (1973) suggest a climax role for P. sitchensis on alluvial habitats, in contrast to its seral role throughout most of the coastal zone. Fonda (1974), on the other hand, indicates T. heterophylla is the climax species on the older terraces. No evidence exists in our data for a directional change from P. sitchensis to T. heterophylla dominance in the South Fork valley. P. sitchensis was currently replacing itself on both terraces and should maintain, if not actually increase, in importance relative to T. heterophylla. A successional shift to Tsuga dominance is not apparent. This is consistent with Cordes' (1972) findings in valley Picea-Tsuga stands in British Columbia.

Several factors could be responsible for the persistence of Picea in these alluvial forests. Many of the stands were park-like with widely spaced stems and numerous openings ranging up to several hectares in size. Such conditions would be more favorable for Picea which is less shade tolerant than Tsuga. An often-cited factor is grazing by Roosevelt elk which are believed to feed selectively on the Tsuga. The importance of browsing has yet to be demonstrated, however, and could not account entirely for the better survival of Picea reproduction. Picea currently demonstrated superior survival from the smallest size classes, presumably below the size of material typically taken by elk.

It is important to note, however, that within the ages of the stands in the South Fork, T. heterophylla regeneration has been favored relative to that of P. sitchensis. The survivorship curves for both upper and lower terraces show a curious reversal in the abundances of pole-sized individuals of the two species. The reasons for this oscillation in regeneration of the two species is not clear. It could be related to climatic fluctuation or to changes in the population of Roosevelt elk. Elk populations were low early in this century, which might account for the wave of larger-sized T. heterophylla. Age data collected for Tsuga do not support this hypothesis, however (i.e., trees sampled did not originate uniformly in the period 1890 to 1910). Fluctuations of either climate or elk herds could create unstable size structures with oscillations in abundance due to time-lag effects.

The lack of correlation between Fonda's (1974) model and the terrace forests of the South Fork is not surprising. Each terrace valley has had its own history of disturbances since the retreat of the glaciers from the valleys. Flooding patterns have not been identical. Moreover, the South Fork valley is distinctive in the breadth of the valley floor relative to the total width of the drainage. Colluvial and alluvial depositions from the valley walls and tributaries, which might alter the basic patterns in these terrace forests, are much less important in the South Fork than in the main Hoh River valley. For example, Acer macrophyllum groves which were confined to colluvial fans (Fonda 1974) were almost absent in the South Fork. The fire history of the two valleys could also be very different, creating an array of seral stand conditions that correlate poorly.

Results of this study clearly show the importance of logs and decaying wood for forest perpetuation. Recruitment would be sparse, indeed, but for these substrates. The superiority of P. sitchensis logs as a regeneration site remains to be explained. The factors which severely limit regeneration on the forest floor are doubtless many, including competing vegetation and possibly disease. The consequences are clear, however, from the extremely rare seedlings not associated with down logs, stumps, or root mounds. Removal of these materials from terrace stands would clearly limit regeneration.

Implications for lands managed for timber production in the vicinity of the Park are clear. Rotten wood is an important substrate for seedling establishment on cutovers, especially where shrub competition is severe. Rotten logs, stubs, and root wads which are potential sites for seedling establishment should be viewed as assets in regeneration problem areas on the west side of the Olympic Peninsula.

CONCLUSIONS

The mature forests described on terraces in the South Fork of the Hoh River provide an outstanding sample of the valley-bottom stands sometimes referred to as Olympic rainforest. Details of composition and structure do vary in other parts of the South Fork and in the main river drainages of the western Olympic Mountains--main Hoh, Quinault, Queets, and Bogachiel Rivers. Nevertheless, some general conclusions about the valley-bottom forests are possible. Landform is, as indicated by Fonda (1974), of major importance in forest composition and structure. The mature Picea-Tsuga forests are often relatively open. Logs are of overwhelming importance for recruitment of new conifers; nurse logs are an essential structure rather than an interesting novelty. A variety of factors appears to make Picea as much a potential climax species as Tsuga. Roosevelt elk intuitively appear important influences on vegetative composition and dynamics, but quantitative data still are absent.

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